QL 355

UNIVERSITY OF CALIFORNIA PUBLICATIONS

IN

ZOOLOGY

WILLIAM EMERSON RITTER
AND
CHARLES ATWOOD KOFOID
EDITORS

VOLUME 11

WITH 26 PLATES

Smithsonian Institution
JAN 4 1915
National Museum
230913

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY
1912-1914

CONTENTS

PAGES

1. Birds in Relation to a Grasshopper Outbreak in California, by Harold C. Bryant 1–20

2. On the Structure and Relationships of *Dinosphaera palustris* (Lemm.), by Charles A. Kofoid and Josephine R. Michener 21–28

3. A Study of Epithelioma Contagiosum of the Common Fowl, by Clifford D. Sweet 29–51

4. The Control of Pigment Formation in Amphibian Larvae, by Myrtle E. Johnson, with pl. 1 53–88

5. *Sagitta californica*, n. sp., from the San Diego Region, including Remarks on its Variation and Distribution, by Ellis L. Michael, with pl. 2 89–126

6. Pycnogonida from the Coast of California, with Description of Two New Species, by H. V. M. Hall, with pls. 3–4 127–142

7. Observations on Isolated Living Pigment Cells from the Larvae of Amphibians, by S. J. Holmes, with pls. 5–6 143–154

8. Behavior of Ectodermic Epithelium of Tadpoles when Cultivated in Plasma, by S. J. Holmes, with pls. 7–8 155–172

9. On Some Californian Schizopoda, by H. J. Hansen 173–180

10. Fourth Taxonomic Report on the Copepoda of the San Diego Region, by Calvin O. Esterly, with pls. 10–12 181–196

11. The Behavior of Leeches with Especial Reference to its Modifiability. A. The General Reactions of the Leeches *Dina Microstoma* Moore and *Glossiphonia stagnalis* Linnaeus; B. Modifiability in the Behavior of the Leech *Dina microstoma* Moore, by Wilson Gee, with 13 text figures 197–305

12. The Structure of the Ocelli of *Polyorchis penicillata*, by Etta V. Little, with pls. 13–15 307–328

13. Modifications and Adaptations to Functions in the Feathers of *Circus hudsonius*, by Asa C. Chandler, with pls. 16–20 329–376

14. A Determination of the Economic Status of the Western Meadowlark (*Sturnella neglecta*) in California, by Harold C. Bryant, with pls. 21–24, and 5 text figures 377–510

15. Parasynaptic Stages in the Testis of *Aneides lugubris* (Hallowell), by Harry J. Snook and J. A. Long, with pls. 25–26, and 1 text figure 511–528

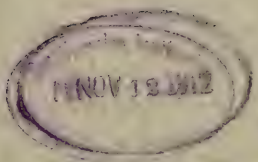
Index 529–538

Errata 538

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY
Vol. 11, No. 1, pp. 1-20 November 1, 1912

BIRDS IN RELATION TO A GRASSHOPPER OUTBREAK IN CALIFORNIA

BY
HAROLD C. BRYANT



UNIVERSITY OF CALIFORNIA PRESS
BERKELEY

UNIVERSITY OF CALIFORNIA PUBLICATIONS

Note.—The University of California Publications are offered in exchange for the publications of learned societies and institutions, universities and libraries. Complete lists of all the publications of the University will be sent upon request. For sample copies, lists of publications or other information, address the Manager of the University Press, Berkeley, California, U. S. A. All matter sent in exchange should be addressed to The Exchange Department, University Library, Berkeley, California, U. S. A.

OTTO HARRASSOWITZ, LEIPZIG.

Agent for the series in American Archaeology and Ethnology, Classical Philology, Education, Modern Philology, Philosophy, Psychology, History.

R. FRIEDLAENDER & SOHN, BERLIN.

Agent for the series in American Archaeology and Ethnology, Botany, Geology, Mathematics, Pathology, Physiology, Zoology, and Memoirs.

ZOOLOGY.—W. E. Ritter and C. A. Kofoid, Editors. Price per volume $3.50. Commencing with Volume II, this series contains Contributions from the Laboratory of the Marine Biological Association of San Diego.

Cited as Univ. Calif. Publ. Zool.

Volume 1, 1902-1905, 317 pages, with 28 plates $3.50

Volume 2 (Contributions from the Laboratory of the Marine Biological Association of San Diego), 1904-1906, xvii + 382 pages, with 19 plates $3.50

Volume 3, 1906-1907, 383 pages, with 23 plates $3.50

A list of titles in volumes 1-3 will be sent on request.

Vol. 4.
1. The Ascidians Collected by the United States Fisheries Bureau steamer *Albatross* on the Coast of California during the Summer of 1904, by William Emerson Ritter. Pp. 1-52, plates 1-3. October, 1907 ..... .50
2. (XVIII)* Behavior of the Starfish *Asterias forreri* de Lorriol, by H. S. Jennings. Pp. 53-185, 19 text figures. November, 1907 ..... 1.00
3. (XIX) The Early Life-History of *Dolichoglossus pusillus* Ritter, by B. M. Davis. Pp. 187-226, plates 4-8. March, 1908 ..... .50
4. Notes on two Amphipods of the Genus Corophium from the Pacific Coast, by J. Chester Bradley. Pp. 227-252, plates 9-13. April, 1908. .30
5. (XX) The Incrusting Chilostomatous Bryozoa of the Western Coast of North America, by Alice Robertson. Pp. 253-344, plates 14-24, May, 1908 ..... 1.00
6. (XXI) On Exuviation, Autotomy, and Regeneration in Ceratium, by Charles Atwood Kofoid. Pp. 345-386, with text figures.
7. (XXII) Notes on some Obscure Species of Ceratium, by Charles Atwood Kofoid. Pp. 387-393.
   Nos. 6 and 7 in one cover. April, 1908 ..... .50
   Index, pp. 395-400.

Vol. 5. (Contributions from the Museum of Vertebrate Zoology.)
1. The Biota of the San Bernardino Mountains, by Joseph Grinnell. Pp. 1-170, plates 1-24. December, 1908 ..... 2.00
2. Birds and Mammals of the 1907 Alexander Expedition to Southeastern Alaska. Pp. 171-264, pls. 25-26, figs. 1-4. February, 1909 ..... .75
3. Three New Song Sparrows from California, by Joseph Grinnell. Pp. 265-269. April 9, 1909 ..... .05
4. A New Harvest Mouse from Petaluma, California, by Joseph Dixon. Pp. 271-273. August 14, 1909 ..... .05
5. A New Cowbird of the Genus *Molothrus*, with a note on the Probable Genetic Relationships of the North American Forms, by Joseph Grinnell. Pp. 275-281, 1 text figure. December, 1909 ..... .05
6. Two New Rodents from Nevada, by Walter P. Taylor. Pp. 283-302, plates 27-29.
7. A Northern Coast Form of the California Gray Fox, by Joseph Dixon. Pp. 303-305.
   Nos. 6 and 7 in one cover. February, 1910 ..... .20
8. Two Heretofore Unnamed Wrens of the Genus Thryomanes, by Joseph Grinnell. Pp. 307-309.
9. The Savannah Sparrow of the Great Basin, by Joseph Grinnell. Pp. 311-316.
10. A Second Record of the Spotted Bat (*Euderma maculatum*) for California, by Joseph Grinnell. Pp. 317-320, plate 30.
    Nos. 8, 9, and 10 in one cover. February, 1910 ..... .15

*Roman numbers indicate sequence of the Contributions from the Laboratory of the Marine Biological Association of San Diego.

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY
Vol. 11, No. 1, pp. 1-20 November 1, 1912

BIRDS IN RELATION TO A GRASSHOPPER OUTBREAK IN CALIFORNIA

BY
HAROLD C. BRYANT

Professor Samuel Aughey, one of the pioneers in economic ornithology, spent twelve years studying the relation of birds to the periodic outbreaks of the Rocky Mountain locust in Nebraska. Over 630 individuals, representing ninety different species of birds, were examined. The investigation showed that "in locust years these insects became the chief food of insect-eating birds, even water-birds devouring them largely." Practically every kind of bird from the tiny kinglet to the huge pelican fed on the locusts to some extent.

The determination of the relation of birds to a grasshopper outbreak in California, where widely different environmental conditions exist, is of interest. It will be seen that the present investigation substantiates the findings of Professor Aughey, and demonstrates that here also birds feed on the insect most available, and are therefore important agents in helping to maintain the balance in nature most suited to the interests of man.

Economic ornithology has progressed to the point where intensive studies are demanded. Each state with its varied environmental conditions should know the economic status of the birds within its borders. California, under the auspices of the State Fish and Game Commission and the University of California, is carrying on an investigation into the food habits of some of the birds of the State about which repeated complaints have arisen from agriculturists and horticulturists. Field investigations in combination with examinations of the stomachs

of birds collected each month of the year in over twenty different parts of the State, are furnishing positive data as to the food of these birds throughout the year. The feeding habits of birds at the time of an insect outbreak, such as that of the differential grasshopper (*Melanoplus differentialis*) which occurred in the San Joaquin Valley in the summer of 1912, afford critical evidence of the value of birds as insect destroyers, and of their part in maintaining that balance in nature most suited to the interests of man.

It is impossible, however, to determine accurately the full value of birds, for we cannot find out what the result would be upon the insect population, if all the birds were suddenly destroyed. Yet a knowledge of their food leads us to conjecture that the destruction of so important an enemy of insects as the birds would result in a great increase in these enemies of vegetation and thus cause a serious disturbance in the balance of nature. The fact that birds destroy large numbers of injurious insects shows them to be important agents in contributing to the safety not only of crops, but also of all vegetation. A realization of the usefulness of birds promotes needed interest in and protection for them.

It is hoped that, as a result of this investigation and others in progress, the insectivorous habits of many of the common birds, and their consequent value, may be more generally known and appreciated by those who most profit by their activities; and also that this study of the relation of birds to a particular outbreak may add something of permanent value to the too meager knowledge of the part played by birds in maintaining the desired balance in nature.

In the investigation here described an attempt was made to answer the following questions:

1. What species of birds in California feed on grasshoppers during the periodical outbreaks of these insects?

2. To what extent does each species at such times feed on grasshoppers as compared with other food?

3. How many, and what proportion, of grasshoppers are destroyed by birds at the time of an outbreak.

4. In what measure may birds be instrumental in preventing and controlling grasshopper outbreaks and what regulatory action may they have at other times?

Certain sections of California are annually troubled with grasshoppers, and there is seldom a year when they do not cause considerable damage in some part of the State. (See Woodworth, 1902, and Hunter, 1905.) Reports of damage caused by grasshoppers in 1912 first began to appear in June. The western part of Merced County, and parts of Kings and Kern Counties, were most affected.

The present investigation was largely carried on in the vicinity of Los Banos, Merced County, this being one of the worst centers of infestation. A comparison of the bird population in the infested area was made possible by a census taken in the vicinity of Merced, a city in the western part of the county.

Alfalfa, pasture, grain, and a little fruit, form the principal crops raised in and near Los Banos. Grasshoppers give some trouble in this vicinity each year, but in 1912 their depredations were more extensive than usual. Grasshoppers were abundant enough to do serious damage in only three districts in the near vicinity of Los Banos. The area most infested is known as "Section Four," one of the ranches of the Miller and Lux Company, eight miles west of the town. The Midway Ranch, four miles east, was badly infested and a slight infestation existed one and a half miles south. On the two ranches mentioned the entire summer crop of alfalfa was destroyed. Burning over of pasture and of alfalfa land was the only control measure resorted to. As most of the grasshoppers already had wings when the burning was done, most of them escaped unharmed. Fields of alfalfa outside of the infested districts looked well, and many of them were being cut.

Garden vegetables and small trees in the infested areas suffered. Corn, tomatoes, and onions were stripped of every leaf. Small shade trees, including eucalyptus, were also defoliated.

A single species of grasshopper, *Melanoplus differentialis,* the differential grasshopper, caused the damage. In pasture land a few grasshoppers of the species *Camnula pellucida* were col-

lected. The only other species noted were *Conozoa behrensi* and *Parapomala calamus*.

Many of the ranchers believed that the grasshoppers had migrated hither from other parts of the county. It appeared, however, that the insects were hatched either in the alfalfa fields themselves or in nearby pasture land. Practically no movement was noted except the usual drifting with the wind when the insects were frightened. Some evidence was obtained that they slowly moved from one alfalfa field to a neighboring one in search of food.

Computation of the numbers per square yard in the infested areas was obtained by counting the numbers disturbed by the observer at each step. Little damage could be noted where the grasshoppers were less than fifteen to the square yard. Where damage was greatest, alfalfa fields averaged about twenty-five to the square yard. In some pasture land along the canals, the numbers were estimated at thirty per square yard.

Los Banos, largely on account of its great irrigation system and the large amount of land which has been swamped, supports a very large bird population. Water-birds and shore-birds are very abundant along the canals and in the marshes, whereas the pasture lands, alfalfa, and the trees, furnish food and cover for many land birds. During the week's stay, July 10 to 17, 1912, twenty-two species of water- and shore-birds were recorded, and forty species of land birds.

A census of birds taken on two successive afternoons on a walk along roads and through fields west of town furnishes one with an idea of the numbers and the comparative abundance of the different species. The first was taken while covering a distance of about three miles, and occupied the time between three and four-thirty o'clock. The second was taken while covering a distance of four miles, and occupied the time between two-thirty and four-thirty o'clock on July 12, both in the same infested territory. Some idea of the bird population in the infested districts compared with that in other parts of the county can be obtained from a third census taken in the vicinity of Merced, in a non-infested region. The counts were made in this instance while driving about twenty miles north and east of Merced. The

time occupied was four hours, one to five in the afternoon. The two regions are similar in the general character of the land and crops, but an error may have been introduced in the censuses, due to the fact that I walked through one region and drove through the other. The larger amount of swamp land in the vicinity of Los Banos also accentuates the contrast in the two censuses.

BIRD CENSUSES

		Number of birds seen in infested areas		in non-infested area
Great Blue Heron	*Ardea herodias herodias*	2	2	....
Anthony Green Heron	*Butorides virescens anthonyi*	3	2	....
Black-crowned Night Heron	*Nycticorax nycticorax naevius*	4	8	. ..
Black-necked Stilt	*Himantopus mexicanus*	2	2	....
Killdeer	*Oxyechus vociferus*	4	29	5
Western Mourning Dove	*Zenaidura macroura marginella*	3	17	13
Burrowing Owl	*Speotyto cunicularia hypogaea*	1	2	....
Red-shafted Flicker	*Colaptes cafer collaris*	....	1	....
Western Kingbird	*Tyrannus verticalis*	9	23	31
Black Phoebe	*Sayornis nigricans*	2	2	1
California Horned Lark	*Otocoris alpestris actia*	2	....	31
Bicolored Red-wing	*Agelaius phoeniceus californicus*	252	290	245
Western Meadowlark	*Sturnella neglecta*	36	67	17
Bullock Oriole	*Icterus bullocki*	8	10	9
Brewer Blackbird	*Euphagus cyanocephalus*	1	4	15
English Sparrow	*Passer domesticus*	6	4	22
Linnet	*Carpodacus mexicanus frontalis*	37	20	34
Green-backed Goldfinch	*Astragalinus psaltria hesperophilus*	....	3	....
Heermann Song Sparrow	*Melospiza melodia heermanni*	4	1	.. .
Western Lark Sparrow	*Chondestes grammacus strigatus*	1	2	3
Western Blue Grosbeak	*Guiraca caerulea lazula*	....	1	. ..
Lazuli Bunting	*Passerina amoena*	....	3	.. .
Cliff Swallow	*Petrochelidon lunifrons lunifrons*	85	66	18
Barn Swallow	*Hirundo erythrogastra*	74	78	56
California Shrike	*Lanius ludovicianus gambeli*	6	14	9
Long-tailed Chat	*Icteria virens longicauda*	3	1	....
Totals		345	649	479
Average number seen per mile		114	162	24
Average number seen per acre		9	13	1—

The figures indicate that the red-winged blackbird was the bird most abundant. Next in order of abundance were cliff swallows, barn swallows, western meadowlarks, linnets, western kingbirds, and shrikes. The difference in the numbers seen per

mile on the two successive afternoons, July 11 and 12, is doubtless due to the fact that on July 12 more of the wooded portion along canals was included, and also to the fact that more flocks of red-wings were seen. That the bird population in the vicinity of Los Banos is at least twelve times that found to be in the vicinity of Merced, is a safe statement. The larger amount of swamp land near Los Banos furnished food and cover for large flocks of red-winged blackbirds and also for many species of water-birds. With increased cultivation and irrigation, and a consequent increase of insect life, the bird population should be expected to increase in the vicinity of Merced.

In determining by observation the birds feeding on grasshoppers, only those birds *actually seen* with grasshoppers in their bills were recorded. The list is as follows:

Western Meadowlark *Sturnella neglecta*
Bicolored Red-wing *Agelaius phoeniceus californicus*
Brewer Blackbird *Euphagus cyanocephalus*
Bullock Oriole *Icterus bullocki*
Western Kingbird *Tyrannus verticalis*
California Shrike *Lanius ludovicianus gambeli*
English Sparrow *Passer domesticus*

The following species, judging from their actions and their food habits, appeared to be feeding on the pests:

Curlew *Numenius hudsonicus?*
Killdeer *Oxyechus vociferus*
Burrowing Owl *Speotyto cunicularia hypogaea*
Swainson Hawk *Buteo swainsoni*
Sparrow Hawk *Falco sparverius sparverius*
Yellow-headed Blackbird *Xanthocephalus xanthocephalus*
Tricolored Red-wing *Agelaius tricolor*
California Horned Lark *Otocoris alpestris actia*
Heermann Song Sparrow *Melospiza melodia heermanni*
Western Lark Sparrow *Chondestes grammacus strigatus*
Barn Swallow *Hirundo erythrogastra*
Cliff Swallow *Petrochelidon lunifrons lunifrons*
Western Bluebird *Sialia mexicana occidentalis*
Western Mockingbird *Mimus polyglottos leucopterus*

Either the same species or closely allied species of these same birds were found by Professor Aughey to feed on grasshoppers. He found that even the goldfinch, known as a strict vegetarian, fed on these insects when they were abundant.

Blackbirds, kingbirds, shrikes, and meadowlarks appeared to be feeding almost wholly upon grasshoppers, and so must be considered among the most efficient destroyers of these insects. Kingbirds, and shrikes, better known as butcherbirds, were constantly seen to catch a grasshopper, carry it to the telephone wires, beat it to pieces, and eat it. The work of these birds and also of blackbirds and orioles was so evident that several ranchers reported these birds as being beneficial in the destruction of grasshoppers.

Although observation in the field furnishes evidence as to the kinds of birds feeding on grasshoppers, and somewhat as to the quantity consumed, yet stomach examination must be depended upon for a verification of the observations made and for dependable evidence as to the numbers of insects taken. Since the mandibles of grasshoppers pass through the alimentary tract undigested, and since they can also be found in the faeces, the number of grasshoppers eaten by a bird is easily determined by counting these hard parts found in the stomach. Some experiments with nestling birds, made by me in the spring of 1912, showed the time of digestion in young meadowlarks to be between two and four hours. Young birds were starved for several hours, and then fed on grasshoppers, beetles, etc. After certain periods of time the birds were killed and their stomachs examined. After two hours most of the soft parts of the grasshoppers were digested, and at the end of four hours, nothing but a few hard parts remained in the stomach. It was found that it took longer to digest grain. The number of insects found in the stomachs of the smaller birds, at least, represents, therefore, the number eaten by the bird within four hours of the time the bird was killed. Experiments by other investigators have shown the time of digestion in birds as large as the crow to be about the same as that determined by me for the meadowlark. At this rate, the number of grasshoppers destroyed in a day must be at least three times as great as the number found in the stomach.

Only a few birds of each species were examined, but even these small numbers should give a fairly accurate idea of the extent to which birds in the infested areas were feeding on

grasshoppers. Most of the birds were collected where grasshoppers were abundant, but a few were taken in non-infested districts so that a comparison might be made. All were collected between the hours of eight and four. The accompanying table, on page 9, gives the results of the stomach examinations.

The burrowing owl must be considered the most efficient destroyer, since parts of twenty-eight grasshoppers were found in the one stomach examined. Blackbirds and meadowlarks, however, because of the large numbers of individuals, were doing the most effective work.

The comparative destruction of grasshoppers per day by single individuals, and by the total number of each species, is represented in the following table:

COMPARATIVE DAILY DESTRUCTION OF GRASSHOPPERS BY BIRDS

Species	Class	Average number of grasshoppers per day by one bird	Average number of grasshoppers per day by total population	Relative destruction of different species represented by lines
Anthony Green Heron	B	42	1,050	
Killdeer	B	33	5,445	
Burrowing Owl	A	84	1,260	
Western Kingbird	D	8	1,280	
Black Phoebe	D	9	180	
California Horned Lark	D	8	88	
Bicolored Red-wing	B	29	78,590	
Western Meadowlark	B	48	24,720	
Bullock Oriole	B	45	4,050	
Brewer Blackbird	D	9	225	
English Sparrow	D	2	100	
Cliff Swallow	D	3	2,265	
California Shrike	C	12	1,200	
Destruction per square mile by total bird population			120,445	

TABLE SHOWING STOMACH CONTENTS OF BIRDS EXAMINED

	Number of stomachs	Kind of field	Time of day	Per cent animal food	Per cent vegetable food	Number of grasshoppers	Per cent of grasshoppers
Great Blue Heron	1	Marsh land	Found dead	100	.....	2 gophers	
Killdeer	1	Pasture	10:10	100	.....	11	100
Anthony Green Heron	1	Pasture	4:00	100	.....	14	15
Burrowing Owl	1	Pasture	12:30	100	.....	28	90
Western Kingbird	2	Pasture, alfalfa	2:00, 10:30	100	.....	5	67.5
Black Phoebe	1	Alfalfa	4:00	100	.....	3	50
California Horned Lark	2	Pasture	12:20	52.5	47.5	5	7.5
Yellow-headed Blackbird	1	Tules	2:00	15	85	....	....
Bicolored Red-wing	4	Alfalfa & pasture	8–4	94	6	38	81.2
Tricolored Blackbird	1	Alfalfa	4:00	97	3	6	97
Western Meadowlark	5	Pasture & alfalfa	8–12	99.2	.8	80	96.2
Bullock Oriole	2	Orchard	9:50	98	2	30	92
Brewer Blackbird	1	Pasture	.....	95	5	3	80
English Sparrow	2	Wheat field	4:00	3.5	96.5	1	2
Cliff Swallow	4	Pasture	8, 4	100	....	2	7.5
Barn Swallow	1	Pasture	12:30	100	.....	.....	....
California Shrike	2	Pasture & alfalfa	10, 11	100	....	8	47

Class A represents birds taking an average of over 50 grasshoppers per day; class B, 25–50; class C, 10–25; and class D, fewer than 10 grasshoppers.

The comparative numbers of the different species of birds were calculated by averaging the two censuses taken in the infested area, and using the average per square mile as a multiplier. Although the table is probably far from accurate, yet it gives some idea of the comparative destruction afforded by the different species, and so its use here seems justified. It will be noted that such birds as the red-winged blackbird and the meadowlark, birds of small capacity, far outrank in destructiveness birds with larger individual capacity, because of their greater numbers. The total destruction caused by the bird population known to feed on grasshoppers must be 120,500 per square mile per day at the minimum.

In the cultivated districts western meadowlarks were very abundant. It was estimated that they averaged from two to the acre in some places, to ten or more in more favorable localities. In alkali pasture land far from water, they did not average more than one or two to the square mile. The stomachs examined showed an average of sixteen grasshoppers per stomach, and one bird had eaten at least twenty-five. On the average, a meadowlark must have consumed at least fifty grasshoppers a day. That means that theoretically a single bird, if it were possible, would clean up about three square yards of the worst infested areas a day, and nearly five square yards in the least infested areas where damage was not serious.

If the infested areas averaged four meadowlarks to the acre, it would take these four birds 406 days to destroy every grasshopper on that acre, assuming no increase in the number of insects. At this rate it can be seen that meadowlarks are unable, and even the whole present bird population, wholly to prevent or control such an outbreak, even though the number of insects consumed is very large. And yet the numbers destroyed meant a diminution of the infestation and therefore a diminution of the damage done.

The bicolored red-wing was the bird most abundant. Large flocks of from one to four hundred individuals were often seen

busily engaged in catching grasshoppers. At times these flocks were seen at a considerable distance from their usual habitat. They appeared to feed almost wholly in the infested districts, and more often in alfalfa fields than in pasture land.

Brewer blackbirds were occasionally seen about ranch houses. Their numbers were few compared with the red-wings. The insectivorous habit of this bird cannot be judged from the one stomach available. That this species fed on grasshoppers to a larger extent than did the red-wing can be safely concluded from the results of other investigations. In an investigation of a butterfly outbreak in northern California (Bryant, 1911), it was found that Brewer blackbirds fed on the butterflies to a far greater degree than did the red-wing, which, under the circumstances, appeared to be largely a vegetarian.

One of the most important things which came out in the investigation was the evidence that at least one of the herons and one of the shore-birds had turned their attention to the insect most abundant. An Anthony green heron, collected along a canal, contained fourteen grasshoppers. One hundred per cent of the food of a killdeer was made up of grasshoppers, eleven having been eaten. The killdeer, being a common bird in the locality, and having a greater capacity than smaller birds, must be considered an effective destroyer.

The stomach of a great blue heron found dead beneath an electric power line, contained no grasshoppers, but did contain two gophers (*Thomomys angularis*), still undigested. It is evident, therefore, that this bird must require at least the equivalent of two gophers a day, for the time of digestion cannot be more than six hours. The testimony of the ranchers of the State also indicates that the great blue heron is one of the best known gopher destroyers.

The California shrike, or butcherbird, seems to have something of a preference for crickets (*Gryllus*), for although this insect was comparatively uncommon, yet the two stomachs examined contained a total of six of these insects, as well as parts of eight grasshoppers.

Stomach examination of two English sparrows collected in a wheat field showed plainly their food preference for grain. Al-

though grasshoppers were abundant on all sides of a small patch of grain, yet these birds were picking the kernels from the heads instead of turning their attention to grasshoppers.

Western lark sparrows, although no stomachs were examined, were doubtless feeding on grasshoppers. Professor Aughey found as many as thirty-eight in one of the stomachs of these birds. Dr. Judd says of this bird: "The lark sparrow is, with the exception of the dickcissel and grasshopper sparrow, the most valuable grasshopper destroyer of all the native sparrows. More than half of its animal food (14 per cent of the total) consists of these insects, and in June they constitute 43 per cent of the diet."

Both barn and cliff swallows were nesting in great numbers under every bridge, and bridges over the canals in that region are numerous. The stomachs of four cliff swallows examined contained a total of two grasshoppers and that of the barn swallow contained none. As swallows feed on rather small insects, it seems natural that they should not feed to any great extent on insects so large as the adult grasshoppers. When these insects were smaller, a larger percentage of the food of these birds may have been made up of grasshoppers. Professor Aughey records having found as many as forty-nine locusts in a single stomach of a cliff swallow, and as many as thirty-seven in the stomach of a barn swallow.

The Bullock oriole, usually condemned for its fruit-eating propensities, was found to be a very efficient destroyer of grasshoppers. Two stomachs contained a total of thirty grasshoppers, ninety-eight per cent of all the food taken by these two birds.

Nighthawks are well known as destroyers of grasshoppers. None were seen, but a reliable observer informed me that they were abundant in certain localities in the vicinity of Los Banos. The U. S. Biological Survey has found as many as sixty grasshoppers in the stomach of one of these birds.

On one ranch, about 2,000 tame ducks were herded over the infested alfalfa fields. The destruction of the grasshoppers by the ducks was so great that an enterprising poultryman with young ducks for sale headed an advertisement in the local paper with a statement in large letters of the number of grasshoppers

daily destroyed by this flock of ducks. The owner of the ducks claimed that from 300 to 400 of the pests were consumed daily by each duck. From 200 to 250 were actually counted in the crops of some of the ducks examined.

Since the time of the Mission Fathers, when grasshoppers were first recorded as giving trouble, these insects have continued their ravages. The bird population during that time has undergone a considerable change. Certain water- and shore-birds, many of them known to be efficient grasshopper destroyers, and especially important because of their migratory habits, have been greatly reduced in numbers. On the other hand certain land birds, owing to a better food supply and cover, have increased in number. Perhaps the most notable example of this increase is to be found in the meadowlark, a bird which feeds almost entirely on grasshoppers when they are abundant. It seems reasonable to believe that the increase of birds has in part, at least, paralleled whatever increase of grasshoppers may have been due to the increased food supply furnished by man. But in spite of what the birds have accomplished in the destruction of these insects, they continue to give trouble. Consequently we should not be justified in saying that birds are capable of controlling all grasshopper plagues so as to prevent damage.

There is danger of overestimating the real economic value of birds at the time of an insect outbreak. On the other hand, however, there is little danger of overestimating the economic value of birds when insects are in normal numbers.

Evidence of the danger in the first instance is afforded in a type of presentation sometimes used in the endeavor to show the economic value of a bird. This type of presentation if applied to the subject in hand would read something like this: The number of grasshoppers destroyed by a flock of 200 red-winged blackbirds working in the infested areas was great. Computation shows that such a flock must have destroyed about 500 grasshoppers an hour, and at least 5,000 in a day. This means that such a flock could theoretically clear up an equivalent of 200 square yards of the worst infested area a day, and almost an acre and a half in a month. The loss of two crops of alfalfa on the same acre means a loss to the rancher of at least $20.

A flock of 200 blackbirds must be, under the circumstances, worth $20 at the minimum. If the value of this same flock of blackbirds be estimated at $100 for the year, they would be able to eat over twenty-five sacks of grain, and yet in the end cause a saving that would more than pay for the grain.

Some of the fallacies which can be easily pointed out in this type of presentation are as follows: In the computation birds are represented as being able entirely to clean up a certain area. This cannot be true, for grasshoppers are taken over a large area and the territory is not cleaned up systematically but enough are usually left to continue some damage. This investigation showed that in spite of the good work of all the birds combined, the grasshoppers took the entire summer crop of alfalfa in local areas. Then, too, birds do not always choose the same locality where damage is done to carry on their beneficial work of insect destruction.

I would not minimize in the least the value of birds at the time of an insect outbreak. The fact that the numbers consumed by birds increased, together with the fact that birds flocked to the infested areas, sufficiently proves their value at such times. I would, however, call attention to the fact that birds are of as great, if not greater, economic value when insects are in normal numbers.

It is at the time of an insect outbreak that the usefulness of birds is most appreciated, because then it is most evident. Their value as insect destroyers is doubtless almost as great, if not greater, throughout the year when outbreaks do not occur.

Fortunately material collected at Los Banos the same month in 1911 was available for comparison. This afforded a comparison of the food of both meadowlarks and bicolored red-winged blackbirds in two successive years, one without and one with an outbreak of grasshoppers. As grasshoppers were far less numerous in the summer of 1911 it has been possible to obtain information as to the comparative destruction by these birds when grasshoppers were in relatively normal numbers, and when they were in abnormal numbers. A glance at the following table shows percentages of the different kinds of food taken, and the average number of grasshoppers taken per bird in the two years.

Western Meadowlark

Number birds	Date	Animal food	Vegetable food	Average no. of grasshoppers per bird	Total per cent grasshoppers
10	July 11, 22, 1911	99.0	1.0	7	83.1
5	July 15, 17, 1912	99.2	.8	16	96.2

Bicolored Red-wing

6	June 22; July 6, 1911	83.5	16.5	2	37.0
4	July 13–16, 1912	96.0	4.0	9	81.2

Meadowlarks took very nearly the same percentage (99, 99.2) of animal food each year, showing that at this time of year the bird is almost wholly insectivorous. The availability of grasshoppers as a diet appears to have influenced the birds taken in 1912, for they averaged sixteen grasshoppers apiece as against seven taken by birds collected in 1911. A greater difference in kind of food is to be noted in the case of the red-winged blackbirds. The number of grasshoppers taken per bird is comparatively smaller than in the meadowlark, as is also the percentage of food made up of these insects.

As the numbers of grasshoppers in 1911, compared to the numbers in 1912, is not definitely known, it is impossible to state whether these birds changed their food habits in response to the extreme availability of the insect in 1912. It is also impossible to state whether the numbers taken in 1912 were in direct proportion to the numbers taken in 1911 or whether they failed to respond to the change in insect population. The fact remains, however, that meadowlarks and red-winged blackbirds, and probably all other insectivorous birds, not only took greater numbers of grasshoppers when they were abnormally abundant but also forsook certain usual articles of diet, such as beetles and weed seeds, thus causing an increased percentage of grasshoppers to be taken as food. The direction of the change in food habits was, however, coincident with that in food supply.

A considerable percentage of the food of insectivorous birds each year is made up of grasshoppers. This shows that grasshoppers are taken as food when they are in small numbers as well as when they are extremely abundant. Even though it be found that the proportion which this particular kind of food

forms of the total food taken by the bird population is less when the insects are in normal numbers, yet it is possible that this small amount of destruction is more important as a means of check than a larger proportion in the food taken when the insects are in abnormal numbers. The average number of grasshoppers, when in normal numbers, per square yard probably does not exceed two or three, and as a rule is probably less. The bird population, though taking but a tenth as many grasshoppers at such a time, would be taking a far greater percentage of the total number of these insects than when taking the numbers found to be consumed during the outbreak. A smaller number of grasshoppers destroyed at the time of minimum numbers has a more important bearing on the prevention of an increase than a larger number destroyed at the time of maximum numbers. We can safely infer, therefore, that the regulative influence of birds is just as important throughout the year as during an insect outbreak, or even more important.

The failure of birds to check an insect outbreak after insects have appeared in abnormal numbers, is evident to all. Their success in preventing insects from becoming abnormally abundant is not at once so apparent. No convincing demonstration of their good work in this connection is obtainable for lack of control experiments. Their constant regulative action must be inferred from data regarding the food of birds and their relation to insects when they appear in abnormal numbers. Judging from all the evidence obtainable, we are justified in believing that birds exert an important regulative influence on insect life throughout the year. And this regulative influence appears to keep pace with the fluctuations of insect life. The importance of birds because of their regulative influence on insects, therefore, although more apparent at the time of an insect outbreak, is no less important when insects are to be found in normal numbers.

Emphasis can well be placed on the fact that a diminution of the numbers of an injurious insect must cause a corresponding diminution of the damage done. If twenty grasshoppers are causing damage on a square yard of alfalfa the loss of even two

must cause some diminution in the amount of damage done, however slight it may be. Consequently the large numbers of grasshoppers taken by birds during the outbreak must have meant a decrease in the possible damage in spite of the fact that such a decrease could not be noted.

It seems safe to say that as a natural control measure, birds must head the list. Parasites in some instances may be more important than birds as natural control measures. However, their influence, owing to their great fluctuation in numbers and delay in their appearance until large numbers of their hosts are assembled, does not appear to be so dependable. Birds can be considered an almost constant factor and therefore must be considered more dependable. None of the grasshoppers collected during the investigation was found to be parasitized

The investigation showed that the birds in the vicinity of the outbreaks changed their food habits, in that they fed on the insect most available. The fact that meadowlarks neglected their usual percentage of ground beetles and fed almost entirely on grasshoppers can be explained in two ways. Either the grasshoppers were taken in preference, or they were taken because they were the most easily obtained. The large number eaten by the killdeer, and by the Anthony green heron, horned lark, and oriole demonstrates this point, for the recorded food of these birds under other conditions does not show so large a percentage of grasshoppers.

Undoubtedly birds flocked to the infested areas. Brewer blackbirds were seen flying out from the ranch houses to the infested areas to feed. Large flocks of bicolored red-wings fed almost entirely in the areas where grasshoppers were abundant. A census of birds taken in infested areas, compared with one taken in a non-infested district, showed birds to be about three times as abundant in the infested areas during hours of feeding. Certain birds examined, and found to contain but few grasshoppers, doubtless fed to a larger extent on these insects when they were of smaller size. The swallows, for instance, owing to their small size, are unable to eat a large grasshopper. If the investigation could have covered the entire time of the out-

break, it would probably have been found that certain birds were far more efficient destroyers when the insects were small than when they became large.

The stomach examination brought out clearly the warfare which is waged by birds on insects, when the latter become abnormally abundant. The destruction which actually goes on is too little appreciated. More records of the good work accomplished could be made available if people would observe more closely. Information as to the exact regulative influence of birds in keeping the numbers of insects below the point where they cause damage, is very desirable. This can be determined only by coöperative observation of many intelligent observers, especially at times of insect outbreaks.

My sincere thanks are due Professor C. A. Kofoid and Mr. Joseph Grinnell, of the University of California, for their helpful criticism of the present paper.

SUMMARY

An investigation into the relation of birds to a grasshopper outbreak was carried on at Los Banos, Merced County, California, July 11 to 17, 1912.

Grasshoppers were found to be causing considerable damage to alfalfa and vegetables. An infestation of about fifteen grasshoppers to the square yard appeared to be necessary to cause noticeable damage. In the infested areas, the grasshoppers were computed to number from twenty to thirty to the square yard.

Observation showed the following species of birds to be feeding on grasshoppers: bicolored red-wing (*Agelaius phoeniceus californicus*), western meadowlark (*Sturnella neglecta*), Brewer blackbird (*Euphagus cyanocephalus*), Bullock oriole (*Icterus bullocki*), western kingbird (*Tyrannus verticalis*), California shrike (*Lanius ludovicianus gambeli*), and the English sparrow (*Passer domesticus*).

Stomach examinations showed all those observed to feed on grasshoppers to be effective destroyers of the pest, and also demonstrated that the following birds were also feeding on grasshoppers: burrowing owl (*Speotyto cunicularia hypogaea*), kill-

deer (*Oxyechus vociferus*), Anthony green heron (*Butorides virescens anthonyi*), black phoebe (*Sayornis nigricans*), California horned lark (*Otocoris alpestris actia*), tricolored red-wing (*Agelaius tricolor*), and cliff swallow (*Petrochelidon lunifrons lunifrons*).

The efficiency of the different species, when determined by destructive capacity, showed the burrowing owl to be the ablest destroyer; when determined by the numbers of individual birds in the territory, showed blackbirds, meadowlarks, killdeer, orioles, and shrikes to take positions in the order named.

Birds cannot be considered a dependable means of control of all grasshopper epidemics, but can be inferred to be efficient in the prevention of many.

Birds can be depended on to act as defenders and protectors of crops because of their warfare against grasshoppers, and their value in this regard can be estimated in dollars and cents.

Birds flocked to areas where grasshoppers were abundant.

Birds changed their food habits and fed on grasshoppers, the insect most available in this case.

The failure of birds to check an insect outbreak is evident to all. Their success in preventing insects from becoming abnormally abundant is not so apparent but is no less real. All obtainable evidence, however, points to the fact that the regulative influence exerted by birds when insects are to be found in normal numbers, although less apparent, is none the less important, for at such times artificial control measures are seldom used.

Certain birds, such as the blackbirds, kingbird, oriole, and meadowlark, although usually condemned for their depredations on crops, in this instance were praised for their usefulness. Damage caused by birds at one time of the year may be more than counterbalanced at another time.

BIBLIOGRAPHY

Aughey, Samuel

1878. Notes on the nature of the food of the birds of Nebraska. First Annual Report of the U. S. Entomological Commission, Appendix II, pp. 13–62.

Beal, F. E. L.

1907. Birds of California in relation to the fruit industry. Part I. U. S. Dept. Agric., Div. Biol. Surv. Bull., no. 30, pp. 1–100, 5 pls.

1910. Birds of California in relation to the fruit industry. Part II. *Ibid.*, no. 34, pp. 1–96, 6 pls.

Bryant, H. C.

1911. The relation of birds to an insect outbreak in northern California during the spring and summer of 1911. The Condor, **13**, 195–208, 4 figs. in text.

Hunter, J. S.

1905. Studies in grasshopper control. Univ. of Calif. Publ., Agric. Exp. Sta. Bull., no. 170, 1–23, 17 figs. in text.

Judd, S. D.

1901. The relation of sparrows to agriculture. U. S. Dept. Agric., Div. Biol. Surv. Bull., no. 15, pp. 1–98, 4 pls., 19 figs. in text.

Kirby, Wm., and Spence, Wm.

1858. An introduction to entomology (7th ed., Longmans, Brown, Green, Longmans, and Roberts, London), pp. xxviii, 607.

Riley, C. V., Packard, A. S., and Thomas, C.

1878. First Annual Report of the U. S. Entomological Commission, pp. 1–295, 5 pls., 111 figs. in text.

1880. Second Report of the U. S. Entomological Commission, pp. 1–322, 17 pls., 10 figs. in text. Appendices I-VII, pp. 1–80.

Webster, F. M.

1907. The grasshopper problem and alfalfa culture. U. S. Dept. Agric., Bureau of Ent., Cir. 84, pp. 1–10, 8 figs. in text.

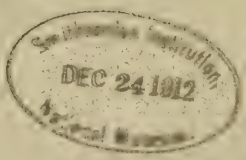
Woodworth, C. W.

1902. Grasshoppers in California. Univ. of Calif. Publ. Agric. Exp. Sta. Bull., no. 142, pp. 1–36, 17 figs. in text.

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY
Vol. 11, No. 2, pp. 21-28 December 6, 1912

ON THE STRUCTURE AND RELATIONSHIPS OF *DINOSPHAERA PALUSTRIS* (Lemm.)

BY
CHARLES ATWOOD KOFOID AND JOSEPHINE RIGDEN MICHENER



UNIVERSITY OF CALIFORNIA PRESS
BERKELEY

UNIVERSITY OF CALIFORNIA PUBLICATIONS

Note.—The University of California Publications are offered in exchange for the publications of learned societies and institutions, universities and libraries. Complete lists of all the publications of the University will be sent upon request. For sample copies, lists of publications or other information, address the Manager of the University Press, Berkeley, California, U. S. A. All matter sent in exchange should be addressed to The Exchange Department, University Library, Berkeley, California, U. S. A.

OTTO HARRASSOWITZ,
LEIPZIG.

Agent for the series in American Archaeology and Ethnology, Classical Philology, Education, Modern Philology, Philosophy, Psychology, History.

R. FRIEDLAENDER & SOHN,
BERLIN.

Agent for the series in American Archaeology and Ethnology, Botany, Geology, Mathematics, Pathology, Physiology, Zoology, and Memoirs.

ZOOLOGY.—W. E. Ritter and C. A. Kofoid, Editors. Price per volume $3.50. Commencing with Volume II, this series contains Contributions from the Laboratory of the Marine Biological Association of San Diego.

Cited as Univ. Calif. Publ. Zool.

Volume 1, 1902-1905, 317 pages, with 28 plates $3.50

Volume 2 (Contributions from the Laboratory of the Marine Biological Association of San Diego), 1904-1906, xvii + 382 pages, with 19 plates $3.50

Volume 3, 1906-1907, 383 pages, with 23 plates $3.50

A list of titles in volumes 1-3 will be sent on request.

Volume 4, 1907-1908, 400 pages, with 24 plates $3.50

A list of titles in volumes 1-4 will be sent on request.

Vol. 5. (Contributions from the Museum of Vertebrate Zoology.)

1. The Biota of the San Bernardino Mountains, by Joseph Grinnell. Pp. 1-170, plates 1-24. December, 1908 ..... 2.00
2. Birds and Mammals of the 1907 Alexander Expedition to Southeastern Alaska. Pp. 171-264, pls. 25-26, figs. 1-4. February, 1909 ..... .75
3. Three New Song Sparrows from California, by Joseph Grinnell. Pp. 265-269. April 9, 1909 ..... .05
4. A New Harvest Mouse from Petaluma, California, by Joseph Dixon. Pp. 271-273. August 14, 1909 ..... .05
5. A New Cowbird of the Genus *Molothrus*, with a note on the Probable Genetic Relationships of the North American Forms, by Joseph Grinnell. Pp. 275-281, 1 text figure. December, 1909 ..... .05
6. Two New Rodents from Nevada, by Walter P. Taylor. Pp. 283-302, plates 27-29.
7. A Northern Coast Form of the California Gray Fox, by Joseph Dixon. Pp. 303-305.
   Nos. 6 and 7 in one cover. February, 1910 ..... .20
8. Two Heretofore Unnamed Wrens of the Genus Thryomanes, by Joseph Grinnell. Pp. 307-309.
9. The Savannah Sparrow of the Great Basin, by Joseph Grinnell. Pp. 311-316.
10. A Second Record of the Spotted Bat (*Euderma maculatum*) for California, by Joseph Grinnell. Pp. 317-320, plate 30.
    Nos. 8, 9, and 10 in one cover. February, 1910 ..... .15
11. Mammals of the 1908 Alexander Alaska Expedition, with Descriptions of the Localities Visited and Notes on the Flora of the Prince William Sound Region, by Edmund Heller. Pp. 321-360, plates 31-32.
12. Birds of the 1908 Alexander Alaska Expedition, with a Note on the Avifaunal Relationships of the Prince William Sound District, by Joseph Grinnell. Pp. 361-428, plates 33-34, 9 text-figures.
    Nos. 11 and 12 in one cover. March, 1910 ..... $1.00
    Index, pp. 429-440.

Vol. 6. 1. (XXIII) On the Weight of Developing Eggs. Part I, The Possible Significance of Such Investigations, by William E. Ritter; Part II, Practicability of the Determinations, by Samuel E. Bailey. Pp. 1-10. October, 1908 ..... .10

2. (XXIV) The Leptomedusae of the San Diego Region, by Harry Beal Torrey. Pp. 11-31, with text figures. February, 1909 ..... .20

---

* Roman numbers indicate sequence of the Contributions from the Laboratory of the Marine Biological Association of San Diego.

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY

Vol. 11, No. 2, pp. 21-28 December 6, 1912

ON THE STRUCTURE AND RELATIONSHIPS OF *DINOSPHAERA PALUSTRIS* (Lemm.)

BY

CHARLES ATWOOD KOFOID AND JOSEPHINE RIGDEN MICHENER

In 1907 Lemmermann described from the plankton in the ponds on the moors of Brandenburg a small spheroidal dinoflagellate which he called *Gonyaulax palustris*. His figures give a clear analysis of the skeletal structure of the species and enable one to establish its relationships. Not having seen material of this species I included it provisionally in the list of species assigned by me to the genus *Gonyaulax* in my monograph (1911a) allocating it in non-fusiform group designated as the subgenus *Gonyaulax*. By the kindness of Dr. Lemmermann, who has courteously placed his type collection at my disposal, a reëxamination of his species has been possible with the result that it now seems necessary to exclude the species from *Gonyaulax* and place it in a new genus *Dinosphaera*.

The skeletal morphology of the genus *Gonyaulax* as defined by me (1911a) and of *G. palustris* as described by Lemmermann, as here analysed by us, is summarized in the following table:

	Genus *Gonyaulax*	*G. palustris*	
		Lemmermann	Kofoid and Michener
Apicals	1–6	3 (and Rautenplatte)	3
Anterior intercalary	0–3	0	1
Precingulars	6	6	6
Girdle	6	?	6
Postcingulars	6	5	5
Posterior intercalary	1	1	0
Antapical	1	1	1

The differences between Lemmermann's analysis and our own are of two kinds: first, those resulting from a different interpretation and allocation of certain plates; and second, those resulting from an extension of the analysis to the plates in the girdle and ventral area. A comparison of Lemmermann's interpretation and our own will be facilitated by reference to his figures here reproduced (figs. 1–5), and those (figs. 6–8) giving our own analysis.

The differences between Lemmermann's analysis and our own of the epitheca are wholly those of interpretation and allocation. In the genera *Gonyaulax* and *Peridinium* the "Rautenplatte" or apical 1′ of my nomenclature, is the midventral plate of the apical series and is normally in contact with the so-called apical pore. In *Dinosphaera* there is no apical pore and apical 1′ is much foreshortened and the dorsal intercalary 1^a correspondingly enlarged, so that the structural apex (*ap.*, fig. 6) or region where the apicals converge is pushed over upon the ventral face and the point of convergence of the anterior intercalary 1^a and the two dorsal apicals 2′ and 3′ occupies the functional apex of the skeleton. Lemmermann calls the anterior intercalary an apical and designates the ventral apical as the "Rautenplatte."

The girdle plates, 1–6, are six in number, as in *Gonyaulax*, a short plate at the proximal junction of girdle and ventral area (*int. pl.*) being regarded as belonging to the ventral area. Lemmermann figures three of the girdle sutures, but does not otherwise specify the number of the girdle plates.

The hypotheca of *Gonyaulax* is uniformly composed of six postcingulars, one posterior intercalary, and one antapical. Lemmermann states that there are five "Postequatorialplatten," one accessory plate, and one antapical. Since the additional postcingular in *Gonyaulax* discovered by me (1911a) is always a minute plate formerly overlooked, it seemed to me probable that it would be found in *G. palustris*. This expectation, combined with Lemmermann's (1907) statement that an accessory plate occurred in the hypotheca, led me (1911a) to retain *G. palustris* in the genus *Gonyaulax*. Our examination of the skeleton, however, fails, with the closest scrutiny, to reveal the least trace of the homologue of the minute postcingular 1′″ of *Gonyaulax*.

The postcingular series in *Dinosphaera* begins with the large plate, the homologue of postcingular 2′ ″ of *Gonyaulax*, and there are but five postcingulars in all, exactly as stated by Lemmermann. On the other hand we find absolutely no trace of any posterior accessory plate. Lemmermann distinctly states that such a plate is present, but his figures 1, 4, and 5 do not delineate it. It is possible that one of the subdivisions (called by us the posterior plate) of the ventral area (Langsfurche) on the lower margin of his figure 5 was accidentally interpreted by him as an accessory plate. We find no homologue to the posterior accessory of *Gonyaulax* in *Dinosphaera* and no grounds for interpreting the posterior plate of the ventral area as the posterior accessory. Lemmermann's ventral view (fig. 1) does not clearly integrate this region as a distinct plate.

Since *Gonyaulax palustris* thus lacks two of the three essential plate characteristics of the genus *Gonyaulax* in the most conservative part of the skeleton it seems necessary to provide otherwise for its classification. We accordingly propose the new genus *Dinosphaera* for its reception and append herewith a brief description, including therein a few additional facts concerning the structure of the girdle and ventral area and our analysis of the skeleton.

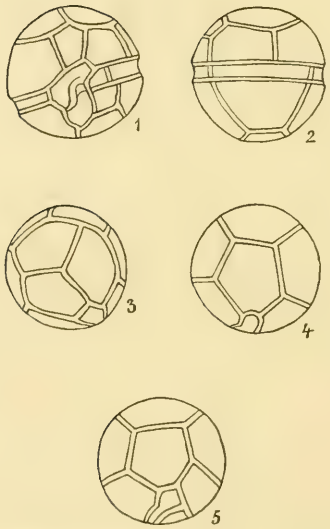
Dinosphaera gen. nov.

Skeleton consisting of an apical series of plates, six precingulars, six girdle plates, five postcingulars and one antapical. Type species *D. palustris* (Lemm.)

Dinosphaera palustris (Lemm.) Kofoid and Michener

Diagnosis.—Body subspheroidal, girdle almost equatorial, slightly displaced distally. Ventral area shallow, widened anteriorly to 0.3 transdiameter. Plate formula 3′, 1^a, 6″, 6, 5′ ″, 0^p, 1″ ″. No apical pore. Surface smooth, sparingly porulate.

Description.—Body subspheroidal, length not exceeding 1.05 transdiameters, dorso-ventral and transverse diameters equal.



Figs. 1–5. *Gonyaulax palustris* from Lemmermann (1907). Fig. 1. Ventral view. Fig. 2. Dorsal view. Fig. 3. Apical view. Fig. 4. Antapical view. Fig. 5. Antapical view somewhat more from the ventral face. × 750.

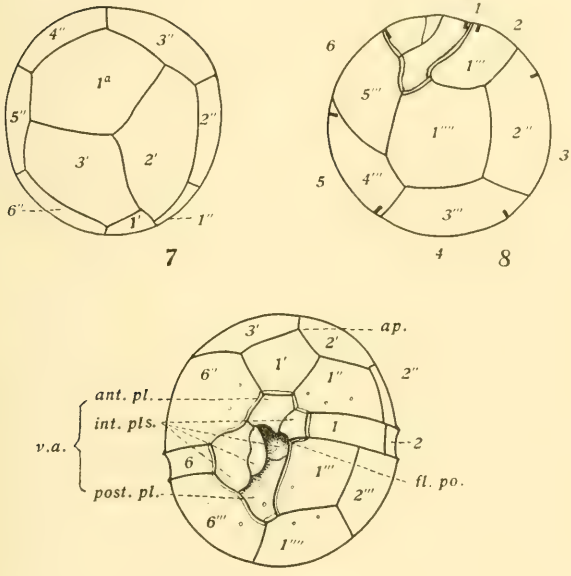


Fig. 6. Ventral view of *Dinosphaera palustris* (Lemm.) Kofoid and Michener. × 1400. From material supplied by Dr. Lemmermann.

Fig. 7. Apical view of same, somewhat from the dorsal side. × 1400.

Fig. 8. Antapical view of same. × 1400.

1–6, girdle series of plates, indicated by peripheral figures on fig. 8, and location of sutures between plates by short heavy radial lines; 1′–3′, apical series; 1ª, anterior intercalary: 1″–6″, precingular series; 1′ ″–5′ ″, postcingular series; 1″ ″, antapical plate; *ant. pl.*, anterior plate of ventral area; *ap.*, apex; *fl. po.*, flagellar pore; *int. pls.*, intermediate plates of ventral area; *post. pl.*, posterior plate of ventral area. The limits of the ventral area are indicated by double lines.

Girdle slightly postequatorial, descending, displaced distally less than a girdle width, if at all, scarcely indented, without lists or prominent ridges or ribs. Epitheca hemispherical, a trifle larger than hypotheca. No apical region differentiated.

The ventral area foreshortened, triangular, widening anteriorly to 0.3 transdiameter. Its total length is little more than a transdiameter. It is curved slightly towards the left of the body posteriorly, not deeply impressed, and without heavy ridges or lists.

Apical plates three, the midventral 1′ wider than long in ventral view, pentagonal, meeting 2′ and 3′ at the point homologous to the apex of *Gonyaulax* at a point about 30° ventral to the apical pole. Posteriorly apical 1′ meets the anterior plate (*ant. pl.*) of the ventral area, and thus parts precingulars 1″ and 6″. Dorsal apicals 2′ and 3′ are large plates uniting with a third somewhat larger plate 1^a, the anterior intercalary, a little dorsal to the apical pole of the skeleton. This relationship has led Lemmermann (1907) to designate these three as apical plates.

The six precingulars 1″–6″ are subequal, except 1″, which is somewhat smaller, and 3″, which is larger than the others.

The girdle plates 1–6 have the same arrangement as in *Gonyaulax*. The much widened ventral area provides anteriorly for the admission of one of its intermediate plates into the proximal end of the girdle adjacent to the flagellar pore. It, as well as another plate of the group, has in this species by virtue of position and prominence a claim to be considered as belonging to the girdle series, but comparison with conditions as found by me (1911a, 1911b) in various species of *Gonyaulax* and in *Spiraulax* lead to the conclusion that the six plates 1–6 are the homologues of the girdle plates in these genera and that the other two belong to the intermediate group of the ventral area.

There is no posterior intercalary plate. Both postcingular 1′ ″ and the antapical 1″ ″ are comparatively large in this species and it seems probable that the former includes the surface usually occupied by the posterior intercalary plate in related genera. The hexagonal antapical is not indented by the ventral area.

The ventral area is peculiar in this species in that its anterior part spreads laterally at the girdle, attaining a width of 0.3

transdiameter, and thus displaying more plainly than usual its constituent plates. The most anterior of these (*ant. pl.*) is notched on its postmargin by the flagellar pore and is the homologue of a similar plate in *Gonyaulax* in which also it abuts anteriorly against apical 1′. The most posterior moiety is an elongated plate (*post. pl.*) upon the left (of the body) side just reaching to the antapical. Between the anterior and posterior plates extends a series of four intermediate plates (*int. pls.*) The first lies in the proximal end of the furrow adjacent to the flagellar pore. The second is a thin scale on the posterior floor of the pore region. The third is a narrow bar on the right side of the pore and the fourth is a large, broadly exposed platelet lodged in the distal end of the girdle. Four intermediate plates have been recognized by me (1911a) in various species of *Gonyaulax,* where they usually lie in a more posterior location than in *Dinosphaera.* The condensation of the hypotheca which has resulted in the suppression of postcingular 1′″ and posterior intercalary 1^p is also accompanied by a shoving forward of the intermediate plates and their spreading out in the girdle region.

The surface is devoid of all spines, lists or ornamentation of any sort. The pores are few and mainly grouped about the ventral area, nearly a dozen in all appearing on the ventral face. Numerous small chromatophores and yellowish oil droplets are present.

Thus far reported only (Lemmermann, 1907) from ponds on the moors of Brandenburg, in association with desmids, *Peridinum umbonatum* Stein, and *P. achromaticum* Levander.

Dimensions.—Length, 27–34 μ; transdiameter, 25–31 μ; width of girdle, 4μ.

Relationships.—*Dinosphaera* is one of the Ceratiinae related to *Gonyaulax* by certain skeletal characters, such as the six precingulars, six girdle plates, and one antapical. In the presence of but a single antapical it resembles also *Amphidinium, Peridiniella,* and *Spiraulax.* Other genera of this subfamily have two, three, or four antapicals (see Kofoid and Michener, 1911). The reduction of the postcingular from six to five plates and the obliteration of the posterior intercalary might well be consequent upon the skeletal concentration attendant upon the spheroidal

form and the slightly smaller size of the hypotheca as compared with the epitheca. A compensating expansion of the ventral area is also evident.

Zoological Laboratory,
University of California.

Transmitted, October 4, 1912.

LITERATURE CITED

Kofoid, C. A., and Michener, J. R.
1911. Reports on the scientific results of the expedition to the Eastern Tropical Pacific, in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer "Albatross," from October, 1904, to March, 1905, Lieut. Commander L. M. Garrett, U. S. N., commanding. XXII. New genera and species of dinoflagellates. Bull. Mus. Comp. Zool. Harvard College, **54**, 265–302.

Kofoid, C. A.
1911a. Dinoflagellata of the San Diego Region, IV. The genus *Gonyaulax* with notes on its skeletal morphology and a discussion of its generic and specific characters. Univ. Calif. Publ. Zool., **8**, 187–286, pls. 9–17, 5 figs. in text.
1911b. Dinoflagellata of the San Diego Region, V. On *Spiraulax*, a new genus of the Peridinida. Univ. Calif. Publ. Zool., **8**, 295–300, pl. 18.

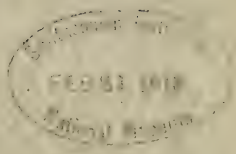
Lemmermann, E.
1907. Brandenburgische Algen, IV. *Gonyaulax palustris* Lemm., eine neue Susswasser-Peridinee. Bot. Centralbl. **21**, 296–300, 5 figs. in text.

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY
Vol. 11, No. 3, pp. 29-51 January 30, 1913

A STUDY OF EPITHELIOMA CONTAGIOSUM OF THE COMMON FOWL

BY
CLIFFORD D. SWEET

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY



UNIVERSITY OF CALIFORNIA PUBLICATIONS

Note.—The University of California Publications are offered in exchange for the publications of learned societies and institutions, universities and libraries. Complete lists of all the publications of the University will be sent upon request. For sample copies, lists of publications or other information, address the Manager of the University Press, Berkeley, California, U. S. A. All matter sent in exchange should be addressed to The Exchange Department, University Library, Berkeley, California, U. S. A.

OTTO HARRASSOWITZ, LEIPZIG.

Agent for the series in American Archaeology and Ethnology, Classical Philology, Education, Modern Philology, Philosophy, Psychology, History.

E. FRIEDLAENDER & SOHN, BERLIN.

Agent for the series in American Archaeology and Ethnology, Botany, Geology, Mathematics, Pathology, Physiology, Zoology, and Memoirs.

ZOOLOGY.—W. E. Ritter and C. A. Kofoid, Editors. Price per volume $3.50. Commencing with Volume II, this series contains Contributions from the Laboratory of the Marine Biological Association of San Diego.

Cited as Univ. Calif. Publ. Zool.

Volume 1, 1902-1905, 317 pages, with 28 plates $3.50

Volume 2 (Contributions from the Laboratory of the Marine Biological Association of San Diego), 1904-1906, xvii + 382 pages, with 19 plates $3.50

Volume 3, 1906-1907, 383 pages, with 23 plates $3.50

A list of titles in volumes 1-3 will be sent on request.

Volume 4, 1907-1908, 400 pages, with 24 plates $3.50

A list of titles in volumes 1-4 will be sent on request.

Vol. 5. (Contributions from the Museum of Vertebrate Zoology.)

1. The Biota of the San Bernardino Mountains, by Joseph Grinnell. Pp. 1-170, plates 1-24. December, 1908 ..... 2.00
2. Birds and Mammals of the 1907 Alexander Expedition to Southeastern Alaska. Pp. 171-264, pls. 25-26, figs. 1-4. February, 1909 ..... .75
3. Three New Song Sparrows from California, by Joseph Grinnell. Pp. 265-269. April 9, 1909 ..... .05
4. A New Harvest Mouse from Petaluma, California, by Joseph Dixon. Pp. 271-273. August 14, 1909 ..... .05
5. A New Cowbird of the Genus *Molothrus*, with a note on the Probable Genetic Relationships of the North American Forms, by Joseph Grinnell. Pp. 275-281, 1 text figure. December, 1909 ..... .05
6. Two New Rodents from Nevada, by Walter P. Taylor. Pp. 283-302, plates 27-29.
7. A Northern Coast Form of the California Gray Fox, by Joseph Dixon. Pp. 303-305.

   Nos. 6 and 7 in one cover. February, 1910 ..... .20
8. Two Heretofore Unnamed Wrens of the Genus Thryomanes, by Joseph Grinnell. Pp. 307-309.
9. The Savannah Sparrow of the Great Basin, by Joseph Grinnell. Pp. 311-316.
10. A Second Record of the Spotted Bat (*Euderma maculatum*) for California, by Joseph Grinnell. Pp. 317-320, plate 30.

    Nos. 8, 9, and 10 in one cover. February, 1910 ..... .15
11. Mammals of the 1908 Alexander Alaska Expedition, with Descriptions of the Localities Visited and Notes on the Flora of the Prince William Sound Region, by Edmund Heller. Pp. 321-360, plates 31-32.
12. Birds of the 1908 Alexander Alaska Expedition, with a Note on the Avifaunal Relationships of the Prince William Sound District, by Joseph Grinnell. Pp. 361-428, plates 33-34, 9 text-figures.

    Nos. 11 and 12 in one cover. March, 1910 ..... $1.00

    Index, pp. 429-440.

Vol. 6. 1. (XXIII) On the Weight of Developing Eggs. Part I, The Possible Significance of Such Investigations, by William E. Ritter; Part II, Practicability of the Determinations, by Samuel E. Bailey. Pp. 1-10. October, 1908 ..... .10

2. (XXIV) The Leptomedusae of the San Diego Region, by Harry Beal Torrey. Pp. 11-31, with text figures. February, 1909 ..... .20

---

*Roman numbers indicate sequence of the Contributions from the Laboratory of the Marine Biological Association of San Diego.

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY
Vol. 11, No. 3, pp. 29-51 January 30, 1913

A STUDY OF EPITHELIOMA CONTAGIOSUM OF THE COMMON FOWL*

BY
CLIFFORD D. SWEET

CONTENTS

PAGE
Introduction 29
Clinical Features 32
Pathology 36
Immunity 40
Complement Fixation 43
Conclusions 48
Literature Cited 49

INTRODUCTION

Economic Importance.—From an economic standpoint epithelioma contagiosum is a disease of considerable interest. In certain localities, notably in the Hawaian Islands, and South Africa, it is one of the chief obstacles to the profitable raising of poultry. It attacks young fowls, is very contagious and proves fatal in a large percentage of the fowls attacked. In California it is apparently less widespread and seemingly has not so great a mortality percentage as in the above-mentioned countries. However, even here, a clear understanding of the epidemiology of the disease, with the control such a knowledge would give of its incidence and spread, would be of very considerable economic value.

* Submitted to the Department of Zoology, in partial fulfillment of the requirements for the degree of Master of Science, in the University of California, April 22, 1912.

Scientific Importance.—In addition to its economic significance, epithelioma contagiosum is a disease of unusual scientific interest, not only because of the obscure nature of its etiology, but because of its apparent relationship or resemblance to other diseases. Because of the epithelial hyperplasia, which is one of the most striking features of the disease, there has been a tendency to classify the lesions produced as neoplasms. Because of the presence of a filterable virus and cell inclusions resembling those of human molluscum contagiosum, variola and vaccinia, it has been classified as one of the exanthemata, and its exciting agent reputed to be a protozoan, in common with many other diseases of this class. Again many others as Friedberger and Fröhner (1908), Schmid (1909), Sigwart (1910), and Kinsley (1907) assert that epithelioma contagiosum and avain diphtheria are different manifestations of the same disease, varying only in clinical features and in nature of, or severity of infection with the same causative agent. This latter contention is based on the fact that in many cases fowls present the clinical features of both diseases simultaneously, and that by inoculation with material taken from chickens having apparently one disease, both diseases may be produced.

With the hope of throwing some further light on the cause and nature of this most interesting disease, the following study was attempted. It is necessarily incomplete and leaves many points requiring further investigation. However, perhaps others may be led to give their attention to further studies of this disease, because of some of the data here presented. The investigations here reported were carried on under a grant from the Federal Adams fund, of the Agricultural Experiment Station of the University of California, for which grateful acknowledgements are here made. The work has been under the direction of Professor Charles A. Kofoid, of the Department of Zoology, and Assistant Professor Clarence M. Haring, of the Veterinary Division of the Agricultural Department, for whose many suggestions and criticisms I am deeply indebted. I should also like to acknowledge the kindly interest shown by Assistant Professor G. Y. Rusk, of the Department of Pathology, and the continual

help I received from my friend, Mr. O. H. Robertson, who was working in the same laboratory on a somewhat similar problem.

History of Disease.—An historical review of the disease hardly seems necessary since it has already been so well done by Reischauer (1906), Burnet (1906), and others. Only a few of the main points will be mentioned in passing. Rivolta (1865) described cellular inclusions, similar to those already described by Virchow in molluscum contagiosum of man. These inclusions he interpreted as gregarines. This was also the classification of Friedberger and Fröhner (1908), who described avian diphtheria as (1) croupous diphtheritic mucous membrane inflammation, the familiar diphtheria of fowls, bacterial in origin, and (2) croupous diphtheritic mucous membrane inflammation in which the mucous membranes of the head give the same clinical picture as in the diphtheria of bacterial origin, but in addition epithelioma contagiosum may appear on the skin of the head, a condition ascribed to the presence of gregarines. Bollinger (1873) characterized the disease as an epithelioma. Marx and Sticker (1902) proved the causative agent of the disease to be filterable through a Berkfeld filter (but not through a Chamberland F filter) and thereby placed it in the great class of diseases which are supposed to be due to ultra-microscopic organisms. They also demonstrated the very great resistance of the virus to heat and chemical agents, finding the dried virus still virulent after being placed in sealed tubes, within a steam sterilizer at 100° C, for an hour. After thirty minutes' exposure to 2% carbolic acid the virus was no longer active, but was active after very long exposure to the action of 1% carbolic acid. They conclude that the cell inclusions are the products of cell degeneration produced by an ultra-microscopic, very resistant virus. Juliusberg (1904) confirmed the filtration results of Marx and Sticker (1902). Borrel (1904) observed granules within the cell inclusions and thought the inclusions were the organic causative agent of the disease. Reischauer (1906) made extensive microscopic studies of the diseased tissue and was of the opinion that the cell inclusions contained the causative agent of the disease and represented development stages of a protozoan. However, it does not seem that he was able to demonstrate a complete life cycle, although

certain of his figures (for example fig. 25) are very suggestive of stages in the development of an organism. He regarded epithelioma contagiosum and avian diphtheria as separate diseases and held that the lesions found on the mucous membranes of the mouth, nasopharynx, and throat in epithelioma contagiosum were extensions to these surfaces of the lesions found on the skin. Burnet (1906) made a study of the morphology of the disease, but came to no definite conclusion from it. In common with earlier writers he placed the period of incubation at about five or six days. He found the blood and internal organs of infected fowls contained the virus, as shown by the fact that he was able to reproduce the disease by inoculation of healthy fowls with the blood and liver of diseased ones. He also produced the disease by allowing fowls to ingest the virus, and by intravenous injection, in each of which methods the lesions appeared at the usual points of election and not elsewhere, except in one case where a typical lesion was found at post mortem in the oesophagus of a fowl which had eaten the virus.

CLINICAL FEATURES

The clinical features of the disease have also been described at length by many writers and we will but sketch them here, making reference chiefly to a few facts in our observations which supplement those recorded by others.

Period of Incubation.—As has been generally noted, the period of incubation is five or six days. However, this varies with the mode of infection and the virulence of the infective material. With virus which had not been attenuated in any way lesions often appeared on the comb and wattles in three days or even sooner after scarification. The same virus when injected intravenously required a longer period of incubation. On the other hand, virus which had been attenuated by age, heat, or chemicals required a greatly lengthened period in which to manifest itself in a macroscopic lesion. These variations in the length of the incubation period are shown in Table I, with the history of the virus used in each case.

TABLE I

History of Virus	Incubation period in days	Growth	Number of fowls inoculated
1. Kept in test tube closed with cotton plug from May, 1909, to July, 1910	7	Small	5
2. Virus used in above after one passage through fowl	(a) 3 (b) 4	Good	(a) 8 (b) 3
3. Kept in test tube closed with cotton plug from May, 1906, to August, 1910	10	Slight	3
4. Mixture of viruses. (a) Kept in test tube closed with cotton plug from May, 1906, to July, 1911, (b) Kept in same manner from August, 1910, to July, 1911	5 & 6	Small and increased in size slowly	4
5. Virus used in No. 4 after one passage through fowl	(a) 4 (b) 6	Fair	(a) 3 (b) 3
6. Virus used in No. 5 after an additional passage through a fowl	(a) 4 (b) 3	Abundant	(a) 6 (b) 1
7. Virus used in No. 6 after an additional passage through a fowl	3	Abundant	6
8. Powdered virus kept in open mortar from August, 1910, to July, 1911	Result, negative		3
9. Virus received from Honolulu—freshly removed from infected fowls	3		6
10. Some virus in No. 9, given intravenously	8 to 12	Lesion appearing first on mucous membranes	3
11. Virus used in No. 7, given intravenously	10 to 12		3
12. Blood from infected fowl, injected intravenously	10	Growth in throat and on comb	1

In those cases in which the incubation period was greatly lengthened by an attenuation of the virulence of the virus, the rate of growth was much slower, although the ultimate course of the disease seemed to be but little changed, this being in accord with the observations of Burnet (1906).

Clinical Course.—When the disease is inoculated by scarifying the comb and wattles there appear after varying periods of inoculation, small, raised, whitish granulations at the points of inoculation. In the early stages these granulations bear a considerable resemblance to tubercles, but later become larger, firmer, more circumscribed, and form a cauliflower-like tumor increasing in size up to about the tenth day. On the tenth to the twelfth day dry scabs form on the surface of the growth, and in the following days the whole growth gradually hardens into a crust, becomes smaller, and at the end of two or three weeks is readily

removed or falls off leaving a core of granulation tissue. This core soon shrivels and disappears, leaving little or no scar.

Intravenous Inoculation.—When inoculation is by intravenous injection, the period of incubation is greatly lengthened, but otherwise the clinical course is unchanged.

Mucous Membrane Inoculation.—If the mucous membranes of the mouth be inoculated small spongy masses form at the point of inoculation. These break down to form cheesy masses (probably from secondary infection) and in some measure resemble the membrane of diphtheria. In about one half our cases these patches appeared on the mucous membranes of the mouth and throat following an inoculation by scarification of the comb, although the mucous membranes were left entirely intact in the operation. In about an equal number of cases the disease ran its entire course without the mucous membranes showing any change whatever (inoculation being by scarification of the comb and wattles).

Relationship of Virulence of Virus to Resistence of Host.—It would seem that the occurrence of lesions is, or is not limited to the point of inoculation by the relation which exists between the resistance of the host and the virulence of the virus used. Naturally such a relationship is difficult to determine, but our results are at least strongly suggestive of its existence. If a small amount of a weakened virus was used and the area of sacrification was small, the lesion produced did not spread beyond the original area of scarification, and remained small throughout the course of the disease which was somewhat shortened. If a large amount of the same weakened virus was used, but the area scarified was large, a large growth was produced, although in no case was a growth noted except at the seat of the original inoculation. When the infective agent has a lowered virulence the period of incubation is prolonged, the manifestation of the disease is limited entirely to the site of ingress, the course of the disease may be shortened, and there is no clinical evidence of any general constitutional effect except an immunity to further infection with the same agent. It seems that this observation is of considerable importance in determining the nature of the disease and must be taken as a strong reason for believing epithelioma contagiosum to be an infectious disease.

Mildness of Inoculated Disease.—In a series of over fifty inoculations, where the virus was unmixed with roup, no fatal terminations were seen except in two cases, in which the vitality was greatly lowered by excessive bleeding. These two fowls became moribund and were killed. At autopsy the internal organs were normal as were the mucous membranes of the head and throat. Cultures taken from the depths of the growths on the comb and from the ventricles of the heart, gave a growth of an organism that was probably *Staphylococcus albus*. This would suggest that death was due to a terminal infection, the portal of entry being the lesions on the head. These findings conflict with those of Reischauer (1906), who found the heart blood sterile in a considerable number of cases, and are too few in number to be more than suggestive. With the exception of these two cases, at no time during the course of the disease were the fowls very much disturbed, as they continued to take food and in every other way to act normally. As Cary (1906) and others have pointed out, the disease is not often fatal except in young fowls. The fowls we used were for the most part nearly grown. However, our records lead us to believe that the disease is a much milder one than roup and that much of the mortality which has been attributed to it may be due to the simultaneous occurrence of the two diseases. Of course, it is also possible that our percentage of mortality was lowered by the virus used (although several were used) being less active than that used by others, or it may be that the climate at Berkeley is unfavorable to the development of the disease. The fact that a number of strains of virus were used would render the first supposition improbable and we can hardly believe too great weight should be given the latter factor.

Epidemiology.—Epithelioma contagiosum is evidently contracted directly. Burnet (1906) has shown that it can be contracted by ingestion of the virus, that the virus is present in the blood stream, and that the typical disease can be produced by intravenous injection. We have confirmed his experiments showing the virus to be present in the blood stream, by injecting blood from a diseased fowl into a normal fowl, and thereby producing specific lesions, not only on the mucous membranes, but also at the usual sites on the comb and wattles. We are

inclined to believe the infection spreads largely by the ingestion of virulent material, as we have seen fowls eat the scabs which fall to the ground and also pick them from the heads of their infected neighbors.

PATHOLOGY

Introduction.—The etiological agent of epithelioma contagiosum has long been thought to be contained in the cell inclusions mentioned by every one who has studied the disease. There is no question but that the causative agent is contained in the epithelial growths since the disease is so readily transmitted by the introduction of even a very minute quantity of the growth into a healthy fowl. Since, from the standpoint of its transmissibility, the disease is so evidently infectious, one would naturally expect to find a specific organism in the lesions produced.

With the above idea in mind, one is naturally struck by the constantly appearing cell inclusions in the epithelial overgrowths. Very similar cell inclusions appear in the cutaneous lesions of variola, vaccine, and human molluscum contagiosum, and are regarded by some as the causative agents of the disease, it being held that they are protozoan in character. Councilman (1904) and his associates have especially emphasized these points, a life cycle having been worked out for *Cytorcytes variolae* by Calkins (1904). In the hope of being able to discover the nature of the cell inclusions in epithelioma contagiosum we examined about four hundred sections from the lesions appearing on the head and on the mucous membranes of the mouth and throat. These sections were taken at varying intervals, mostly from the third to the twelfth day. They were fixed in Zenker's fluid and hardened by the usual methods and stained by the following methods: (1) hematoxylin and eosin; (2) Giemsa's blood stain; (3) Heidenhain's iron haematoxylin and Bordeaux red; (4) Mühlens-Hartmann's vaccine stain; (5) von Wasielewski's stain; (6) Mann's eosin-methylene blue; (7) Osmic acid; (8) Sharlach R; and (9) Levaditi's silver impregnation method. Also a large number of smears were made directly from the tumor growths, fixed with methyl alcohol and stained by the Giemsa method.

Tissue Reaction.—The tissue changes described by Reischauer (1906), Burnet (1906), Apolant (1902), and many others, were noted. These are mainly as follows: There is a marked hyperplasia of the epithelium, the number of cells being greatly increased, and the individual cells being greatly enlarged. The cells apparently increase in number by the usual method, that is, the cells multiply in the stratum germinativum by mitosis and in the portions of the growth removed from the growing layer undergo only secondary changes. It also appears that the growing layer is unequally stimulated, since the proliferating epithelium takes the form of cell nests or buds projecting downward into the underlying connective tissue and upward to form the cauliflower-like growths which appear on the surface of the epithelium. These buds or fingers of epithelial cells, on section, very much resemble in appearance a true epithelioma. They are supported by thin strands of connective tissue, there being considerable hyperplasia of the underlying connective tissue. In the advanced stages of the disease this hyperplasia of connective tissue elements is much more marked. However, the excess connective tissue may in large part be due to the secondary infection which is always present. In addition to the above noted changes there is a marked engorgement of the underlying blood vessels and a considerable wandering of leucocytes into the tissue (including the epithelium) lying about the vessels. Even, in the early stages, before secondary infection has apparently taken place to any marked degree there is the tissue reaction that is present about a focus of infection. In other words, the nature of the tissue reaction speaks strongly for the infectious nature of the disease, varying from the picture presented by the ordinary pyogenic infection only in the unusual reaction of the epithelium. As has been noted, there is an enormous increase in the number of epithelial cells. Besides this, the individual cells become as large as 40 μ in diameter. The epithelial cells lying next the connective tissue are about normal in size, stain deeply and are undergoing rapid proliferation. Their walls are well defined, the cytoplasm dense and finely granular, and the nuclei are normal in appearance. The cells outside the deepest layers in the epithelial bud become progressively larger, stain less

deeply, the cytoplasm becomes pale and less granular; being vacuolated in many cells, the cell walls become less well marked and finally disappear so that the central portion of the nest is a necrotic mass of indistinct cell elements. In the same order, the nuclei are also enlarged, become increasingly vacuolated, contain bizarre clumps of chromatin, stain faintly, the limiting membrane becomes less well defined and finally disappears entirely so that they (the nuclei) are no longer visible.

Cell Inclusion.—Beside the normal cell contents nearly all of the epithelial cells contain the cell inclusion mentioned above. This cell inclusion which occurs so constantly in the epithelial cells, has been thought by many to be analogous to the cell inclusion present in carcinomata and by others to the inclusion seen in the lesions of variola, vaccina, etc. Reischauer (1906) and others have taken it to be an animal parasite, while Burnet (1906), Apolant (1902), and many others thought it to be merely a product of cell degeneration.

Form and Occurrence in Cells.—The cell inclusion is spheroidal or ellipsoidal, usually larger than the nucleus, has fairly definite boundaries, although we were not able to see a definite limiting membrane. It lies in the neighborhood of the nucleus. Usually a single one is found in each cell, the exceptions to this being, first, at times two of these bodies are seen in a single cell; and second, some enlarged cells do not appear to contain any. However, this apparent absence of a cell inclusion is probably due to the inclusion lying outside the plane of the section in the enlarged epithelial cell. Rarely these bodies are seen in intercellular spaces. Apparently these cell inclusions are not present in the epithelial cells which are in process of active proliferation. However, this is a difficult point to determine accurately, because there are cells containing the cell inclusion which lie within the proliferating zone and which do not shown any signs of degeneration. Although these cells do not show any signs of degeneration, only those which do not contain the cell inclusion show evidence of normal active proliferation. At times cells containing the cell inclusion also contain atypical mitotic figures, but on the whole, it seems fairly certain that the appearance of the inclusion in a cell accompanies a cessation of proliferation.

Nature of Inclusion.—It seems that epithelioma contagiosum produces a very rapid proliferation of epithelial cells, those cells which are in a state of proliferation remaining free from visible cell inclusions. This would suggest that this cell inclusion, in its enlarged state at least, appears in a cell only after its birth as an independent cell, and that it is only after the cell is no longer proliferating that the cell inclusion appears. This would at once lead one to label the inclusion as a product of cell degeneration, as Burnet (1906), Apolant (1902), Marx and Sticker (1902) have done for this disease, and as Ewing (1904) has done for the inclusions seen in vaccina. However, the fact that in the neighborhod of the proliferating zone many cells appear which contain well marked cell inclusions, but which show little or no evidence of degeneration, makes one hesitate to make so absolute a conclusion. So if one assumes that the cell inclusion is merely a product of cell degeneration he must assume that it is due to some chemical change within the cell which does not manifest itself as a usual type of degeneration until late in the life of the cell. This does not seem a very difficult assumption to make in view of the very extensive changes produced in the epithelial elements.

Changes in Inclusions.—As mentioned above, in passing from the proliferating zone inward to the center of the epithelial cell nests, progressive degeneration of the cytoplasm and nucleus are seen. Apparently, the same progressive degeneration is seen in the cell inclusions. In the region of the proliferating zone the cell inclusions stain deeply, and are clear cut in outline, but as one goes away from this zone toward the center of the epithelial bud they stain less deeply, have less clearly defined margins, become increasingly vacuolated and finally are completely disintegrated. Here again one is tempted to ascribe all this change to progressive degeneration, but is deterred by remembering that it so very closely follows the normal sequence in the life cycle of protozoan cell parasites. Very often there appear smaller bodies within the cell inclusions, giving them something of a mulberry appearance. This occurs often enough and is so well marked that it very strongly suggests the presence of a stage of sporulation. Also in fixed preparations stained with Giemsa

stain and with hematoxylin and eosin, as well as in fresh smears stained in the same manner, there are small acid staining granules within the epithelial cells which suggest a stage of fragmentation. However, we are not able, at this time, to so relate the changes in the cell inclusions that any conclusive resemblance to a complete protozoan life cycle is produced.

IMMUNITY

All who have worked with the disease have noted the development of a complete immunity. Löwenthal (1906) says this immunity is shortlived, lasting only one to two months, while others, as Reischauer (1906), say it lasts during the lifetime of the fowl. Still others, as Schmid (1909), say it varies with the severity of the original infection. We are not prepared at present to agree or disagree with any of these observations, as the greatest time between original inoculation and an attempted reinoculation which has elapsed in our series is thirty-five days. Complete immunity was present at the end of that time.

Early Immunity Incomplete.—Reischauer (1906) observes that within the first week following the original inoculation there is no immunity, but that later than this a reinfection runs a very light course or is negative. Marx and Sticker (1902) found the immunity complete after twelve days.

Our results, which confirm these latter observations, are given in the following table:

Table II

Time between inoculations	Nature of lesions produced by second inoculation	Result of second inoculation	Number of trials
3 days	Lesions unaltered. Course of disease exactly like that produced by 1st inoculation	Positive	12
6 days	Lesions produced and course of disease changed, but little if at all from normal	Positive	9
9 days	Lesions produced small course of disease shortened and very mild.	Positive	8
12 to 14 days		Negative	15
35 days		Negative	6

Immunity Specific.—The above results were all obtained from a considerable number of cases and show a remarkable agreement. In the cases that were found to be immune after the twelfth day, repeated inoculations, with different strains of virus, were made, but no positive results were obtained. However, in a number of these hyper-immune fowls typical roup was produced by inoculation with another strain of roup-infected virus. Fally (1908) has observed that an immunity to epithelioma contagiosum does not include an immunity to roup, and has argued, therefrom, that each disease is an independent clinical entity. Our results bring us to the same conclusion, and this seems to us one of the strongest reasons for believing the two diseases are due to two distinct causative agents. Seventy-three chickens in all were inoculated. All but ten of these were inoculated with virus which was kept in a test tube, plugged with cotton, from May, 1906, to July, 1910, or with the same strain of virus after one, two, three, or more passages through roup-free fowls. As mentioned above, in some cases the tongues and hard palates were scarified and virulent material rubbed in. In these cases and in about half those in which the comb and wattles alone were inoculated, yellow caseous patches appeared on the mucous membranes of the mouth and throat. However, these patches were well circumscribed in all cases and neither in extent, nor appearance were they typical of roup. Upon examination under the microscope, in the early stages before secondary infection had produced necrotic changes, it was possible to make out changes corresponding exactly to those produced in the epithelium of the comb. There was an hyperplasia of the epithelial layer of the mucous membrane and cell inclusions of the same nature as those seen in the epithelial growths. At no time, so far as we are aware, has any one seen these inclusions in the lesions produced in the mouth by roup. After a few days these patches become necrotic and were made up of epithelial debris and one was unable to longer make out any definite sturucture. The ten chickens, above referred to, were inoculated with virus freshly received from The College of Hawaii, Honolulu, and the lesions of epithelioma contagiosum differed in no way from those produced by our other virus.

Development of Roup in Immune Fowls.—On the same day in which the ten normal fowls were inoculated with the Hawaiian virus, ten hyper-immune fowls were inoculated with the same virus. These immune fowls developed no lesion of epithelioma contagiosum at any time. However, the normal ones developed typical growths of epithelioma contagiosum at the seat of inoculation, in the usual time, and a few days later three of them developed typical sypmtoms of roup. There was profuse purulent discharge from the nose and mouth, the sinuses under the eyes became greatly enlarged, the eyes were swollen, closed and filled with cheesy, white exudate, the fowls refused food, became moribund and died. Within a short time another developed the same symptoms and at the same time two of the immune group, which had given no evidence of epithelioma contagiosum after repeated inoculations, succumbed with typical symptoms of roup. The remainder of those inoculated with the Hawaiian virus recovered in the usual way, without showing any signs of roup. However, since Ward (1905) has shown how difficult it is to transmit roup by inoculation (only one of seventeen being positive in his series), its absence from some of the members of the later group would seem to have no bearing on our conclusions. Our results point rather strongly to the conclusion that we had one strain of the virus of epithelioma contagiosum which was free from roup, and one which was mixed with the virus of roup. Because of our results, we are led to believe that Schmid and others who have apparently obtained both diseases with a single virue, had a mixture of the causative agents of two entirely separate diseases.

POSSIBILITY OF DOUBLE INOCULATION

That the virus of epithelioma contagiosum in the form of the scabs is capable of carrying a second infective agent, is shown by a small series of inoculations we carried out in 1910. Two of the cockerels used had slight purulent discharges from the nostrils, having what is usually termed a cold. These cockerels were inoculated with epithelioma contagiosum and later material was taken from them and four other cockerels inoculated. Each

of these four developed a cold exactly similar to the one present in the original hosts, in addition to the lesions of epithelioma contagiosum. Eight other cockerels inoculated with the same virus except that it had been passed through healthy cockerels, were entirely free from any symptoms of a cold.

COMPLEMENT FIXATION

From the fact that an immunity is developed, it occurred to us that during the course of the disease there might be a specific antibody developed in the blood. Following this idea we carried on complement fixation tests on the blood of normal and infected fowls.

Preparation of Material.—After the usual manner, rabbits were immunized against the red blood cells of sheep, and the haemolytic amboceptor thus obtained titrated and preserved in a dark place. An antigen was prepared from the tumors produced on the combs of fowls by epithelioma contagiosum, and from the liver of a fowl having epithelioma contagiosum, after the method of Michaelis and Lisser. Fresh complement or alexin was obtained daily by bleeding guinea pigs. Blood was taken from a sheep every other day, defibrinated, centrifuged, and the corpuscles washed four times in physiological salt solution. Blood was taken from normal and diseased fowls under as nearly as possible aseptic conditions and allowed to stand on ice for from 12 to 24 hours. The clear serum was then pipetted off, and inactivated for 30 minutes at 57° C. in a water bath. After careful titration of the alexin amboceptor and antigen, the factors of our haemolytic system were now assembled and were mixed according to table No. 3.

Technique of Bleeding Fowls.—The technique used in obtaining the blood from the fowls may be of interest, because we have not been able to find a similar method described in the literature, and it was only after trying several unsatisfactory methods that we hit upon this method. It is not necessary to kill the fowls, as considerable quantities of blood can be taken without damaging the bird, and they can be bled rather frequently as they show marvelous powers of recuperation. Even

when a fowl is bled to the point of weakness, he soon recovers and after a lapse of a few days seems to have nearly replaced the lost blood. The wing was raised from the body, and the feathers plucked from the under surface which was then cleaned with 1% trieresol. The fowl was laid upon its side, being held down by the left forearm of the operator while the upper wing was grasped and extended backward by the left hand. Then with small, sharp-pointed scissors, a small incision was made in the brachial artery or vein just where it passes over the flexor surface of the elbow. If only a small quantity of blood was wanted, the vein was opened; while if a larger quantity was needed, the artery was opened. As the vessel was opened the blood welled up into the natural receptacle formed by the elbow and the membrane of the wing. As this anatomical cup filled the blood was drawn up into a sterile Luer hypodermic syringe, without any needle attached, and immediately transferred to a small sterile test tube. A glass Luer syringe is preferable, because it can readily be operated by one hand, and is also readily cleaned, when it is desired to bleed a number of fowls. By following this method, it was found that 5 c.c. or even more, of blood could be taken from a full-grown fowl without causing it any apparent inconvenience. Even when the artery is opened the haemorrhage stops very soon, because of the great coagulability of the blood, and if it does not do so the operator can readily stop it by fairly strong flexion of the wing at the elbow. In a long series of bleedings only two fowls were lost, one from excessive bleeding, and one from an infection of the wing leading to gangrene.

TABLE III

TABLE OF COMPLEMENT FIXATION DATA					AMOUNTS IN CUBIC CENTIMETERS	
	I				II	
	Na Cl	Suspected serum	Antigen	Alexin[1]	Amboceptor	Sheep cells, 5% suspension[2]
1	1	0.1	1	1 cc.	1 cc.	1 cc.
2	2	0.1	..	1 cc.	1 cc.	1 cc.
3	1	0.2	1	1 cc.	1 cc.	1 cc.
4	2	0.2	..	1 cc.	1 cc.	1 cc.
5	1	....	1	1 cc.	1 cc.	1 cc.
6	..	....	2	1 cc.	1 cc.	1 cc.
7	2	...	..	1 cc.	1 cc.	1 cc.
8	2	....	1	.....	1 cc.	1 cc.
9	3	....	..	.....	1 cc.	1 cc.
10	4	....	..	.....	.....	1 cc.

[1] Incubate one hour after thorough shaking.

[2] Incubate 5 to 10 hours after thorough shaking.

Variations in Amounts of Suspected Serum Used.—By adding additional tubes corresponding to tubes 1 and 2, 3 and 4, the quantities of the suspected serum were varied, being added in all quantities from 0.1 to 0.8 c.c. The antigen was found no longer to prevent haemolysis at a dilution of 1 to 100, so was used at a dilution of 1 to 200. The alexin usually produced complete haemolysis at a dilution of 1 to 20 or 1 to 25. The amboceptor was used at a dilution of 1 to 1000, and the sheep cells in a 5% suspension in physiological salt solution.

Complement Fixation.—With normal serum in quantities from 0.1 ccm. up to 0.8 ccm. haemolysis was complete. Haemolysis was usually complete after two hours, and always at the end of five hours' incubation. The same result was obtained with serum taken from infected fowls during the period of incubation. However, a different result was obtained with serum from fowls in which the lesions of epithelioma contagiosum were present. In this serum there was considerable evidence of a specific antibody. Haemolysis did not occur as readily and was almost constantly incomplete at the end of ten hours incubation. The results were not as striking as we believe they could be made by variation in the nature of the antigen, and since there is no question of diagnosis involved will never be of practical value, but it is cer-

tainly of interest as denoting the formation of a specific antibody, or a deviation of complement, in the serum of the infected fowl by an infection of epithelioma contagiosum.

It is also of interest to note, in this connection, that antibodies are most strongly developed in the presence of protozoan infections and that this evidence, in so far as it goes, tends to support the protozoan hypothesis as to the etiological factor in epithelioma contagiosum.

Appearance of Specific Antibody.—While blood was taken from four or five diseased fowls almost daily for a period of almost four weeks, we are not prepared to say definitely at just what stage of the disease the antibody is first present. However, we were unable to find it present to any marked degree until the lesions were fairly well marked, except in those where the method of inoculation was intravenous injection, when it seemed to appear earlier. In any haemolytic system, the addition of normal serum may at times produce fixation, but that this was not so in our series is shown by the contrast between the amount of fixation in tubes, one of which contained serum from a normal healthy fowl, and another of which contained an equal amount of serum from an infected fowl taken under exactly the same conditions. Each set was carefully controlled (see table 3) and on every occasion when the controls indicated that none of the factors of the haemolytic system was at fault, there was uniformly markedly more fixation in the tubes containing serum from fowls having epithelioma contagiosum than in those having like amounts of normal fowl serum. The following are the results of a single day's experiment and are given because they are typical of the results obtained on many days. The numbering of the tubes corresponds to that in table 3.

TABLE IV

1. Serum from normal fowl.

No.	Amount of serum in ccm.	Result
1	0.2	Haemolysis complete
2	0.2	Haemolysis complete
3	0.4	Haemolysis complete
4	0.4	Haemolysis complete
5	0.6	Haemolysis complete
6	0.6	Haemolysis complete

2. Serum from fowl fifteen days after inoculation (lesions on comb well developed).

No.	Amount of serum in ccm.	Result
1	0.2	Some sediment, supernatant fluid cloudy, marked contrast to normal
2	0.2	Haemolysis complete
3	0.4	Considerable fixation
4	0.4	Haemolysis complete
5	0.6	Considerable fixation, marked when contrasted with No. 5, table 1
6	0.6	Slight fixation

3. Serum from fowl eight days after inoculation on comb, lesions extensive, about half as thick as a pea.

No.	Amount of serum in ccm.	Result
1	0.2	Considerable fixation
2	0.2	Nearly clear, haemolysis complete
3	0.4	Considerable fixation
4	0.4	Haemolysis complete

4. Serum from fowl ten days after inoculation on the comb.

No.	Amount of serum in ccm.	Result
1	0.2	Complete haemolysis
2	0.2	Complete haemolysis
3	0.6	Marked fixation
4	0.6	Nearly complete haemolysis

5. Serum from fowl six days after intravenous injection of 1 ccm. of a physiological salt emulsions of ground scabs

No.	Amount of serum in ccm.	Result
1	0.2	Complete haemolysis
2	0.2	Complete haemolysis
3	0.4	Considerable fixation
4	0.4	Complete haemolysis
	Controls Nos. 5, 6 and 7—Complete haemolysis	
	Controls Nos. 8, 9 and 10—No haemolysis	

It would be interesting to compare the haemolytic reactions of the serum from fowls having epithelioma contagiosum and those having roup. Our intention was to do this, but time did not permit. That the fowls used for all our experiments were entirely free from the effects of any former infection of either epithelioma contagiosum or roup was assured by using fowls raised at the University Farm where neither disease exists.

CONCLUSIONS

1. Epithelioma contagiosum is a specific infectious disease.

(*a*) The virus is constantly present in material from the lesions found on the head and on the buccal mucous membranes, and in the blood of infected fowls. The disease is readily and constantly produced by inoculation with material from the lesion or with the blood from infected fowls. This inoculation is not the transplantation of tumor cells from one fowl to another, as the virus is present in the filtrate after passage through a Berkfeld filter, and so far as we are able to discover neoplasms have not been produced by inoculation with such filtered extract, with the exception in one case of a sarcoma of the fowl transmissible by an agent separable from the tumor cells as described by Rous (1911).

(*b*) The period of incubation varies from three to twelve days depending on the virulence of the virus and on the method of inoculation.

(*c*) The virulence of the virus is lowered by age and by the action of chemicals. Within limits the virulence of the virus increases with passage through a fowl.

(*d*) An immunity is produced, which is complete within a definite time, is specific and of considerable duration.

(*e*) The tissue reaction at the point of inoculation is very similar to that produced by inoculation with known infectious agents.

(*f*) There is a definite relation between the resistance of the host and the virulence of the infection, *i.e.*, an inoculation with a virus of reduced virulence produces a reaction that is entirely local, while a more virulent strain produces a reaction that is not limited to the point of ingress.

(*g*) In response to an inoculation with epithelioma contagiosum there is produced a specific antibody in the blood of the host.

2. Epithelioma contagiosum and roup are entirely independent diseases.

(*a*) Epithelioma contagiosum is constantly and readily transmitted by inoculation, while roup is not (Ward).

(*b*) Immunity conferred by an inoculation with the virus of epithelioma contagiosum does not prevent the contraction of roup.

(*c*) Under the conditions of our experiment, epithelioma contagiosum was not fatal to mature fowls, while all that contracted roup died.

3. The cell inclusions present in the hyperplastic epithelial cells of epithelioma contagiosum show changes which may perhaps represent stages in the development of a protozoan parasite, but we are unable to so connect them that a complete life-cycle is definitely established.

LITERATURE CITED

Apolant, H.
1903. Beitrag zur Histologie der Geflügelpocke. Virchow's Arch., **174**, 86–95.

Bollinger, A.
1873. Ueber Epithelioma contagiosum beim Haushuhn und die sogenannten Pocken des Geflügels. Virchow's Arch., 58, 349–361, pl. 9.

Bordet, J. and Fally, V.
1910. The bacterium of fowl diphtheria. Jour. Comp. Path. and Therap., **23**, 565–568.

Borrel, A.
1903. Épithélioses infectieuses et épithéliomas. Ann Inst. Pasteur, **17**, 81–122, pls. 1–6.

Burnet, E.
1906. Contribution a l'étude de l'épithélioma contagieux des oiseaux. Ann. Inst. Pasteur, **20**, 742–765, 1 fig. in text.

Carnwath, T.
1907. Zur Aetiologie der Hühnerdiphtherie und Geflügelpocken. Bull. Inst. Pasteur, **5**, 976–977.

Cary, C. A.
1906. Chicken pox, or sore head in poultry. Bull. Alabama Agr. Exp. Sta., 1906, 21–49. (Bull. No. 136.)

Councilman, T. W., and Calkins, G. N.
1904. Studies on the pathology and on the etiology of variola and of vaccinia. Jour. Med. Research, **11**, 7–361, pls. 1–20.

Ewing, J.
1904. Comparative histology of vaccinia and variola. Jour. Med. Research, **12**, 509–533, pls. 12–15.

Fally, V.
1908. Diphthérie aviare et épithélioma contagieux. Am. Med. Vet., **57**, 69–75.

Friedberger and Fröhner.
1900. Lehrbuch der Speciellen Pathologie and Therapie der Haustheire (Enke, Stuttgart), **2**, 467–480.

Howard, T. H. and Schultz, O. T.
1911. Studies in biology of tumor cells. Monographs Rockefeller Inst. Med. Research, **2**, 1–77, pls. 1–6.

Jowett, W.
1909. Epithelioma contagiosum. Jour. Comp. Path. and Therap., **22**, 22–29.

Kingsley, A. T.
1907. Epithelioma contagiosum. Am. Vet. Rev., **30**, 1438–1443.

Mallory, F. B.
1904. Scarlet fever. Jour. Med. Research, **10**, 334–341, pl. 1.

Moore, V. A.
1906. The pathology and differential diagnosis of infectious diseases of animals (Taylor and Carpenter, Ithaca, N. Y.), **16**, 506, 9 pls. and 110 figs. in text.

Marx, E. and Sticker, A.
1902. Untersuchungen über das Epithelioma Contagiosum des Geflügels. Deutsche Med. Wochenschr., **1902**, 893.
1903. Weitere Untersuchüngen uber die Mitigation des Epithelioma Contagiosum des Geflügels. *Ibid.*, **1903**, 79–80.

Mohler, J. R. and Eichorn, A.
1911. Fixation of complement test for glanders. U. S. Bureau of Animal Industry, Bull. No. 136, 31 pp. 5 pls.

Noguchi, H.
1910. Serum diagnosis of syphilis (Lippincott & Co., Philadelphia and London), vii + 173, 14 figs. in text.

Reischauer, Dr.
1906. Uber die Pocken der Vögel, ihre Beziehungen zu den echten Pocken und ihren Erreger. Centlbl. Bakt., **40**, 356–361, 474–479, 653–681, pls. 1, 2.

Rous, P.
1911. A sarcoma of the fowl transmissible by an agent separable from the tumor cells. Jour. Exp. Med., **13**, 396–411, pls. 38–52.

Salmon, D. E.
1899. Diseases of Poultry (Geo. E. Howard Co., Washington), 248 pp., 71 figs. in text.

Schmid, G.
1909. Untersuchungen über die Beziehung zwischen Geflügeldiphtherie und Epithelioma contagiosum. Centlbl. Bakt., **52**, 200–234, 2 figs. in text.

Sigwart, H.
1910. Experimentalle Beiträge zur Frage der Identität von Geflügeldiphtherie und Geflügelpocken. Centlbl. Bakt., **56**, 428–464.

Ward, A. R.
1905. Observations on roup in chickens. Proc. Am. Vet. Med. Assoc., **1905**, 198–201.

Zoological Laboratory,
University of California.

Transmitted April 24, 1912.

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY
Vol. 11, No. 4, pp. 53-88, pl. 1 March 31, 1913

THE CONTROL OF PIGMENT FORMATION IN AMPHIBIAN LARVAE

BY
MYRTLE E. JOHNSON

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY

APR 21

UNIVERSITY OF CALIFORNIA PUBLICATIONS

Note.—The University of California Publications are offered in exchange for the publications of learned societies and institutions, universities and libraries. Complete lists of all the publications of the University will be sent upon request. For sample copies, lists of publications or other information, address the Manager of the University Press, Berkeley, California, U. S. A. All matter sent in exchange should be addressed to The Exchange Department, University Library, Berkeley, California, U. S. A.

OTTO HARRASSOWITZ, LEIPZIG.

Agent for the series in American Archaeology and Ethnology, Classical Philology, Education, Modern Philology, Philosophy, Psychology, History.

R. FRIEDLAENDER & SOHN, BERLIN.

Agent for the series in American Archaeology and Ethnology, Botany, Geology, Mathematics, Pathology, Physiology, Zoology, and Memoirs.

ZOOLOGY.—W. E. Ritter and C. A. Kofoid, Editors. Price per volume $3.50. Commencing with Volume II, this series contains Contributions from the Laboratory of the Marine Biological Association of San Diego.

Cited as Univ. Calif. Publ. Zool.

Volume 1, 1902-1905, 317 pages, with 28 plates $3.50

Volume 2 (Contributions from the Laboratory of the Marine Biological Association of San Diego), 1904-1906, xvii + 382 pages, with 19 plates $3.50

Volume 3, 1906-1907, 383 pages, with 23 plates $3.50

Volume 4, 1907-1908, 400 pages, with 24 plates $3.50

A list of titles in volumes 1-4 will be sent on request.

Vol. 5. (Contributions from the Museum of Vertebrate Zoology.)

1. The Biota of the San Bernardino Mountains, by Joseph Grinnell. Pp. 1-170, plates 1-24. December, 1908 ..... 2.00
2. Birds and Mammals of the 1907 Alexander Expedition to Southeastern Alaska, by Joseph Grinnell and others. Pp. 171-264, pls. 25-26, figs. 1-4. February, 1909 ..... .75
3. Three New Song Sparrows from California, by Joseph Grinnell. Pp. 265-269. April, 1909 ..... .05
4. A New Harvest Mouse from Petaluma, California, by Joseph Dixon. Pp. 271-273. August, 1909 ..... .05
5. A New Cowbird of the Genus *Molothrus*, with a note on the Probable Genetic Relationships of the North American Forms, by Joseph Grinnell. Pp. 275-281, 1 text figure. December, 1909 ..... .05
6. Two New Rodents from Nevada, by Walter P. Taylor. Pp. 283-302, plates 27-29.
7. A Northern Coast Form of the California Gray Fox, by Joseph Dixon. Pp. 303-305.

   Nos. 6 and 7 in one cover. February, 1910 ..... .20
8. Two Heretofore Unnamed Wrens of the Genus Thryomanes, by Joseph Grinnell. Pp. 307-309.
9. The Savannah Sparrow of the Great Basin, by Joseph Grinnell. Pp. 311-316.
10. A Second Record of the Spotted Bat (*Euderma maculatum*) for California, by Joseph Grinnell. Pp. 317-320, plate 30.

    Nos. 8, 9, and 10 in one cover. February, 1910 ..... .15
11. Mammals of the 1908 Alexander Alaska Expedition, with Descriptions of the Localities Visited and Notes on the Flora of the Prince William Sound Region, by Edmund Heller. Pp. 321-360, plates 31-32.
12. Birds of the 1908 Alexander Alaska Expedition, with a Note on the Avifaunal Relationships of the Prince William Sound District, by Joseph Grinnell. Pp. 361-428, plates 33-34, 9 text figures.

    Nos. 11 and 12 in one cover. March, 1910 ..... $1.00

    Index, pp. 429-440.

Vol. 6. 1. (XXIII) On the Weight of Developing Eggs. Part I, The Possible Significance of Such Investigations, by William E. Ritter; Part II, Practicability of the Determinations, by Samuel E. Bailey. Pp. 1-10. October, 1908 ..... .10

2. (XXIV) The Leptomedusae of the San Diego Region, by Harry Beal Torrey. Pp. 11-31, with text figures. February, 1909 ..... .20

* Roman numbers indicate sequence of the Contributions from the Laboratory of the Marine Biological Association of San Diego.

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY

Vol. 11, No. 4, pp. 53-88, pl. 1 March 31, 1913

THE CONTROL OF PIGMENT FORMATION IN AMPHIBIAN LARVAE*

BY

MYRTLE E. JOHNSON

CONTENTS

PAGE

A. Introduction 53
B. Current theories of pigment formation 54
C. The relation of amount of nutrition to pigmentation 59
D. Effect of various kinds of foods upon pigmentation 64
E. Effect of lecithin and various foods used in experimentation, upon the tyrosinase reaction 69
F. Effect of lecithin upon pigmentation 73
G. Effect of certain other organic substances upon the tyrosinase reaction and upon pigmentation 76
H. Histological differences between chromatophores of larvae fed upon different foods 80
I. Effect of changes in light, heat, and food upon pigmentation 82
J. Summary 83
K. Bibliography 84

A. INTRODUCTION

The experiments considered in this paper grew out of a series of feeding experiments carried on with larvae of *Hyla regilla* and *Rana* sp. While size differences only were considered at first, color differences soon became so marked as to demand attention. The amount of black pigment in the different lots of tadpoles varied considerably and this variation was not correlated with the size of the tadpole. It was apparent that certain foods

* A thesis presented to the Faculty of the College of Natural Sciences, in the University of California, in partial satisfaction of the requirements for the degree of Doctor of Philosophy. April, 1912.

contain elements which govern the formation of pigment independently of the effect of the food upon the size of the organism.

It was found that most of the tadpoles showed a large or medium amount of pigment excepting those that were fed on yolk of egg, which showed a much smaller amount. Experiments showed that when lecithin was fed along with foods which ordinarily produced much black pigment that a much smaller amount of pigment was produced. Experiments with tyrosinase showed that the tyrosinase reaction could in a measure be inhibited by the addition of lecithin or the products of digestion of egg yolk. The experiments thus give an example of a chemical substance inhibiting the tyrosinase reaction and when fed to the tadpoles inhibiting to some extent the production of melanin pigment in the epidermis.

This investigation has been carried on in the zoological laboratory of the University of California under the direction of Professor Harry Beal Torrey, and I am greatly indebted to him for his continued help and encouragement. I also wish to express to Professors T. B. Robertson and H. C. Biddle of this University my thanks for their kind interest and assistance in questions of physiological and organic chemistry.

B. CURRENT THEORIES OF PIGMENT FORMATION

In relating these results to the current theories of color formation and inheritance it will be convenient to consider Weismann's germinal selection theory, aspects of the Mendelian theory of inheritance, and the results of recent biochemical investigation.

Weismann postulates determinants, aggregations of ultimate "vital units" capable of transmission through the germ cells and able to determine "hereditary characters" of the body. Their presence determines the specific development of a particular part of the body which may consist of a group of cells, a single cell or a part of a cell. A struggle for existence between the biophores, the smallest elements composing the determinants, continues throughout the development of the embryo, different biophores being able to appropriate different amounts or kinds of nourishment. These differences in nourishment cause inequalities in the

growth of the different biophores which produce differences in the constitution of the determinants and consequently qualitative variations in the organism. These variations may be spontaneous resulting from intra-germinal nutritive conditions and therefore not affecting all the ids at once or they may be brought about by extra-germinal influences affecting all the ids at the same time.

Among Mendelians the factor hypothesis plays an important role. Castle (1909) names the following color factors which he finds in the case of the gray rabbit:

> "Symbol C. A common color factor necessary to the production of all pigment, wanting only in albinos.
>
> " B. A factor for black, some substance which acting upon C produces black pigmentation.
>
> " Br. A factor for brown, some substance which acting upon C produces a chocolate-brown pigmentation.
>
> " Y. A factor for yellow, some substance which acting upon C produces yellow pigmentation.
>
> " I. An intensity factor, which determines whether the pigmentation shall be intense (as in black and in yellow), dilute (as in blue and in cream), or of some intermediate degree of intensity.
>
> " A. A pattern factor which causes the black or brown pigments to be excluded from certain portions of the individual hairs, where yellow then shows. A "ticked" gray coat results. When this factor is present the under surfaces of the rabbit (tail, belly) are unpigmented (white). The symbol, A, stands for agouti, this factor having first been demonstrated in the "agouti" guinea-pig. (See Castle, 1907.)
>
> " U. A factor for uniformity of pigmentation (in distinction from spotting with white, S).
>
> " E. A factor governing the extension of black and of brown pigmentation, but not of yellow. When most restricted in distribution the black or brown pigments are found in the eye and in the skin of the extremities only, but not in the hair, when more extended they occur also in the hair generally."

The various types of coloration seen in different rabbits are represented by means of various arrangements of these symbols —in fashion resembling the formulae for the constitution of molecules of organic compounds.

As to the form and composition of these Mendelian factors, Castle says we can at present give no satisfactory answer, but he adds (p. 68): "It is, however, we think, not necessary to suppose that there exist in the minute germ-cell as many complex organic substances as there are activities of the cell; neither is it necessary to suppose a different substance present for every independent factor identified. The various independent factors may have a basis no more complicated than that of so many atoms attached to a complex molecular structure. Experiment shows that the factors may be detached one by one from the organic complex. The discontinuity of their coming and going is entirely in harmony with the conception of them as components merely of complex molecular bodies." Such a view attempts to provide for segregation of characters without discussing vital units.

Among the chemists is Dewitz (1902) who experimented with fly larvae (*Lucilia Caesar*) and found that while there was no tyrosinase in very young larvae (one or two days old) older larvae contained a considerable quantity. When the pupae formed they rapidly became pigmented, but this pigmentation could not go on without oxygen.

Phisalix (1905) working with cockroach larvae, found that the larvae when hatched were colorless, but within three hours changed through grey and brown to black. Phisalix concludes that tyrosin and tyrosinase exist in the embryo long before the color develops and that "it is probable that they coexist in the egg or that they are deposited at the time of ovogenesis."

Roques (1909) found that during the metamorphosis of *Limnophilus flavicornis* Fabr., the amount of tyrosinase in the body was greatest just before pigmentation began and as the amount of pigment increased, the tyrosinase decreased, until it was entirely absent when the beetle was fully pigmented.

Riddle (1909, p. 329) reviews our knowledge of melanin color formation and urges the futility of piling up factors one for every color in the germ to explain the production of melaninic color since without them " in an animal that produces melaninic color, *there exists all the machinery necessary to produce a series or scale of these colors.*" He continues (p. 336): "This means that the animal that transmits the enzyme

for black, i.e., produces black-colored offspring must *at the same time* transmit also the enzyme for *brown, chocolate, red, yellow, etc.* (more accurately, an enzyme for each step of oxidation from tyrosin to black melanin), *without the absence of a single one.*" In a footnote (p. 337) he adds: "The sort of specificity of enzymes that has thus far been assumed by the Mendelians has, however, been of a different sort; namely, that for the production of each color only one enzyme is necessary, but the enzyme which produces any particular color is specifically different from those which produce other colors; . . . ."

Riddle (1909, p. 336) maintains that with tyrosinase able to produce a series of colors, several of Castle's factors (A, B, E, I, and D) may be reduced to one, tyrosinase, while C, the chromogen, may be left out entirely as a factor since such a chromogen is "universal in protoplasm." In conclusion he asks: "Is it too much to expect that the further application of such tests as the one here presented in outline for the melanin colors will in the end remove *many* of the Mendelian 'factors' from the germ cells? That many of their 'characters' will come to rest on a more proximate basis; will be known to have their 'determination' and origin in very general germinal powers, and in somatic conditions obtaining previous to, or at the time of, their development?"

Gortner (1910a, 1911a, 1911c) has recently published results of similar investigations on the meal worm, cicada, and potato beetle. He finds that in the meal worm the chromogen is secreted only as needed for pigmentation and is present in exceedingly small amounts at any one time, that tyrosinase is present in both the pupa and beetle, but the chromogen is apparently lacking in the pupa stage, the only stage without pigmentation.

In the case of the periodical cicada, the tyrosinase is not found in the body of the pupa or the adult but is apparently secreted with the new cuticula since the oxidase is present in water in which the newly emerged adults have been washed. In his study of the Colorado potato beetle (*Leptinotarsa decemlineata* Say) Gortner finds the pigmentation "produced by the interaction of an oxidizing enzyme of the tyrosinase type, and an oxidizable chromogen. The color pattern is caused by the

localized secretion of chromogen." Gortner (1911d) after further investigation of different melanins concludes that they are formed by the interaction of an oxidase and an oxidizable chromogen. He finds that there are at least two types of melanin which may be differentiated by their appearance and by their solubility in acids. He thinks it probable that the two types are formed by the oxidation of different chromogens.

Some of these later results, it seems to me, lead one to take a little different view of the situation from the one taken by Riddle. He (1909, p. 334) speaks of the different colors of the tyrosin series as obtainable by different degrees of oxidation, for instance he says: "At present the *biological* data are wanting to quantitatively seriate all of the several colors; but there is apparently enough data to warrant the definite statement that *yellow mice* are forms with the power to oxidize tyrosin compounds to an *intermediate* point." If we adopt this view we are under the necessity of postulating some chemical difference between the oxidase in yellow mice and that in brown mice that causes this difference in oxidation.

The results of Bertrand (1908) and of Abderhalden and Guggenheim (1907, 1908) show that the end result of the series of colors shown by melanin pigment is different when the tyrosin exists in different combinations, or when different chromogens are used. Gortner showed that the spots on the elytra of the potato beetle are due to a localized secretion of the chromogen rather than to a difference in the oxidase which is apparently present over the whole area. It would appear from these facts that slight differences in color between two individuals are due to slight differences in the combination in which the chromogen exists (or existed when the pigment was produced) and that variations in the marking of different individuals are due to slight variations in the character or diffusion of the chromogen in different localities.

The difference in color in the case of the tadpoles here described seems to be brought about by a reduction in the amount of black pigment rather than by a change in the color of the pigment. This reduction in the amount of black pigment allows

the epidermal pigments of other sorts and colors to come into greater prominence.

One must distinguish then between differences in coloration which involve actual differences in the color of one or more of the pigments and those which involve differences in the proportional amounts of the different pigments. Although the inhibitors here discussed merely reduce the amount of melanin, instances cited show that the tyrosinase reaction may be so affected by certain chemical substances that the color of the resulting pigment is different from that of ordinary melanin. The "factors" postulated by Mendelians may operate in this latter fashion, also the chemical substances cited below which are able to change the color of the plumage of birds undoubtedly act in this way.

C. THE RELATION OF AMOUNT OF NUTRITION TO PIGMENTATION

Weismann's view that color is profoundly influenced by nutritive conditions is supported by Tornier's experiments in pigment control. My results with similar experiments, however, do not support this view.

Tornier (1907, 1908), experimenting with *Pelobates* larvae, divided the tadpoles into lots for differential feeding. He found that tadpoles receiving a minimum amount of food (algae, together with varying amounts of fish) contained little or no pigment and that by feeding increased amounts of fish it was possible to change the epidermal coloring from white through yellow, red, and grey, to black. Comparable effects were produced by removing a portion of the yolk from the egg. This reduced the nutrition of the animals and produced albinism, erythrinism, or blackness depending upon the state of nutrition. He also found that the experiments could be carried in the opposite direction and that through a diminution of feeding, well fed black larvae could be changed back through a series of colors in the order of black, brown, red, grey, white. He sought to show not only that increase in food supply caused a greater development of pigment in the chromatophores but also that the pigment

granules of the chromatophores acted as reserve material in cases of inanition.

Experiments similar to these of Tornier were carried on by me during two successive seasons with *Hyla* and *Rana* tadpoles. The results do not confirm those of Tornier, since the tadpoles receiving a small amount of food were no lighter than those receiving an abundance.

The tadpoles from a single egg mass were divided into three lots and each lot given a different amount of food. As it is impossible when feeding graduated amounts of food to be sure that the tadpoles in a given dish share the food alike, instead of placing different amounts of food in the different dishes, the food was withheld from the dishes for different lengths of time. On days when the tadpoles received food they were given as much as they could eat, and on other days all food was removed from the dishes. One set of tadpoles was fed every day, the food of the second set was withheld every third day and that of the third set was withheld every second day. The three sets of tadpoles thus received large, medium, and small amounts of food approximately in the ratio of $1 : \frac{2}{3} : \frac{1}{2}$.

The growth of the tadpoles was proportional to the amount of food received and the amount of pigment seemed also to be proportioned to size since the large, medium, and small tadpoles on the same diet were all of the same color, those that were half starved being *no lighter than those that were large and well fed.* In order that this might not be a prejudiced judgment the different sets of tadpoles were repeatedly submitted to other observers before explaining the object of the experiment. The verdict always was that the tadpoles were all the same color or that the smaller ones were a little darker. The experiments were performed for two successive years with the same result (table 1).

TABLE 1

Length measurements and color of tadpoles fed on different amounts of food. Tadpoles of lots A and B were all the same size when the experiment began Feb. 10, 1912; those of C and D were the same size when the experiment began, April 28, 1911. Length measurements for lots A and B represent average length of all tadpoles in the dish, those for C and D, the average of several typical tadpoles.

A. *Rana* tadpoles fed on liver

Amount of food	Length in mm. Feb. 13	Feb. 20	Mar. 6	Number of tadpoles	Color
Full amount	16.1	21.4	27.4	8	Dark
⅔ full amount	15.4	20.2	24.0	8	Dark
½ full amount	15.6	19.1	22.5	8	Dark

B. *Rana* tadpoles fed on egg yolk

Amount of food	Length in mm. Feb. 13	Feb. 20	Mar. 6	Number of tadpoles	Color
Full amount	15.3	21.3	28.1	8	Light
⅔ full amount	15.0	19.5	24.4	8	Light
½ full amount	15.4	19.1	23.2	8	Light

C. *Hyla* tadpoles fed on liver

Amount of food	Length in mm. May 10	June 3	Number of tadpoles	Color
Full amount	16	30	6	Dark
⅔ full amount	13	23	6	Dark
½ full amount	12	20	7	Dark

D. *Hyla* tadpoles fed on egg yolk

Amount of food	Length in mm. May 10	June 3	Number of tadpoles	Color
Full amount	20	32	4	Medium light
⅔ full amount	14	24	4	Medium light
½ full amount	13	18	5	Medium light

Owing to accidents and the small allowance of food, most of the tadpoles living on half the regular fare died before metamorphosing. I have one preserved specimen, however, which is about half the normal size and hardly more than skin and bones, but is as deeply pigmented as any of the larger specimens.

Tornier's experiments with yolk removal were also imitated with the *Hyla* and *Rana* tadpoles. Here again it was found that the tadpoles which had lost yolk, though smaller than the others,

were not necessarily lighter colored. A part of the yolk was removed from a number of tadpoles by sucking it through a capillary tube. Approximately half of the yolk was removed from the *Rana* tadpoles and a larger proportion from the *Hyla* tadpoles. The yolk was not removed until the embryos were quite large—nearly ready to hatch—so it is probable that in the case of *Hyla* at least, a portion of the alimentary tract was removed with the yolk.

The two lots of *Rana* tadpoles, those from which the yolk had been removed, and the control presented practically the same appearance: both were dark grey, but those which had suffered the loss of yolk were no lighter than the control (table 2).

Table 2

Length measurements of tadpoles from which yolk has been removed. Measurements represent average lengths of all tadpoles in the dish.

A. *Rana* tadpoles. Yolk removed Feb. 2, 1912

	Length measurements in mm. taken					Feb. 26	
	Feb. 6	Feb. 9	Feb. 13	Feb. 20	Feb. 26	Number of tadpoles	Color
Yolk removed	10.3	12.5	13.8	15.0	14.8	8	Medium
Control	9.9	12.2	14.5	14.9	14.9	5	Medium

B. *Hyla* tadpoles. Yolk removed Feb. 19

	Length measurements in mm. taken				Mar. 2	
	Feb. 20	Feb. 22	Feb. 26	Mar. 2	Color	Number of tadpoles
Yolk removed	7.87	9.08 (10 tadpoles)	9.55	9.4	A few somewhat lighter than control	3
Control	8.1	9.51 (10 tadpoles)	10.15	10.05	Medium	9

The two lots of *Hyla* tadpoles showed slight differences. Some of the individuals that had suffered the loss of yolk were as dark as the control tadpoles but others were a little lighter. Microscopical examination shows that these lighter individuals have about the same number of pigment spots, but that some of the spots are smaller and some are a little lighter than those of the control tadpoles.

This difference seems to me to be a direct result of the loss of nourishment—the amount of pigment is less just as the length and width measurements are less and the muscles and other

tissues appear more transparent. The yolk loss has meant to the tadpole a loss of substances from which directly or indirectly pigment is ultimately formed, as well as a loss of tissue forming substance. The very smallness of the differences indicates that they are due to a lack of material for tissues and pigment building rather than to a using up of pigment once formed.

This view is supported by Riddle's investigation of pigment formation in the feathers of young birds. Although there is little definite knowledge concerning the formation of the particular melanins present in this instance or the other cases cited, it is highly probable that they are formed similarly and that they are equally dependent upon or independent of nutrition.

After carrying on feeding experiments with young birds, Riddle (1908) concludes that pigment and barbule forming cells are both reduced in rate of production relative to growth in certain other parts of the feather because of the less favorable relations which the pigment producing cells bear to the nutriment carried by the blood. He says, "In just the same way that a lack of nutrition checks the production of barbule forming cells, it reduces the amount of pigment formed and taken up by the barbule cells."

There is in this instance as in the case of the tadpole, a loss of certain tissue building substances along with a loss of pigment forming substances. The "less favorable relations which the pigment producing cells bear to the nutriment carried by the blood" may make the difference between daily and nightly growth more marked here than in other places but the difference is probably present in other parts though from the nature of the structure it is less easily discovered.

Similarly, in reporting observations on *Amblystoma tigrinum*, Powers (1908, p. 38) says: "I have kept many adults, young and old, for three and even four years, and have subjected them to very varying conditions of nutrition, temperature, etc., and by means of photographs I have compared the appearance of many during successive seasons. Starvation does, of course, produce a marked effect on many organs and upon the animal's whole appearance, save color."

These instances and the results of the experiments all point to the same conclusion, that with reduced nutrition there is a reduced pigment production along with a reduction of tissue or tissue formation with the result in the case of the tadpole that the color of the animal appears neither darker nor lighter.

D. EFFECT OF VARIOUS KINDS OF FOOD UPON PIGMENTATION

Of especial interest in a discussion of the effect of food upon the color of animals are the following classical examples cited by Darwin (1868, vol. 2, p. 337) in *"The Variation of Animals and Plants under Domestication."* He says: "It is well known that hemp-seed causes bullfinches and certain other birds to become black. Mr. Wallace has communicated to me some much more remarkable facts of the same nature. The natives of the Amazonian region feed the common green parrot (*Chrysotis festiva,* Linn.) with the fat of large Siluroid fishes, and the birds thus treated become beautifully variegated with red and yellow feathers. In the Malayan archipelago, the natives of Gilolo alter in an analogous manner the colours of another parrot, namely the *Lorius garrulus* Linn., and thus produce the *Lori rajah* or King-Lory. These parrots in the Malay Islands and South America, when fed by the natives on natural vegetable food, such as rice and plantains, retain their proper colours. Mr. Wallace has, also, recorded (A. R. Wallace, *Travels on the Amazon and Rio Negro,* p. 294) a still more singular fact. 'The Indians (of S. America) have a curious art by which they change the colours of the feathers of many birds. They pluck out those from the part they wish to paint, and inoculate the fresh wound with the milky secretion from the skin of a small toad. The feathers grow of a brilliant yellow colour, and on being plucked out, it is said, grow again of the same colour without any fresh operation."

Romanes (1895, vol. 2, p. 218) cites the above instances of changes in the plumage of birds and the fact also noted by Darwin that canaries become red when fed on cayenne pepper, and adds: "Dr. Sauermann has recently investigated the subject experimentally; and finds that not only the finches, but likewise other birds, such as fowls, and pigeons, are subject to similar

variations of colour when fed on cayenne pepper; but in all cases the effect is produced only if the pepper is given to the young birds before their first moult. Moreover, he finds that a moist atmosphere facilitates the change of colour, and that the ruddy hue is discharged under the influence either of sunlight or of cold. Lastly, he has observed that sundry other materials such as glycerine and aniline dyes, produce the same results; so there can be no doubt that organic compounds probably occur in nature which are capable of directly affecting the colours of plumage when eaten by birds."

These facts indicate that significant variations in color are produced by different *kinds* of food and the following experiments with tadpoles bear out the suggestion.

Both *Rana* and *Hyla* tadpoles were used for these experiments. Different bunches of eggs were separated so that the larvae used for one set of experiments were from a single egg mass. As soon as the tadpoles hatched they were divided into different groups and each group was fed on one kind of food. The water in the dishes was changed every other day and the tadpoles given fresh food. In the later experiments the table and the sides of the dishes were covered with black paper. This allowed the light to enter only from above and insured equal illumination for all the dishes. The foods first used were beef liver, egg yolk, egg albumen, beef suet, brown and white beans, white bread, and fish. The foods were all cooked by boiling and finely divided by being put through a sieve or rubbed between the fingers. A few measurements given in the following tables will show the size relations fairly well. The intensity of the color is also noted (table 3).

Table 3

Length measurements and color of tadpoles fed on different kinds of food. Measurements represent average of several typical tadpoles from each dish.

A. *Hyla.* Experiment started Feb. 18, 1911

	Length in mm.			Number of tadpoles	
Food	April 18		Color	Feb. 18	Apr. 8
Liver	38.0 mm.		Dark	7	3
Yolk	40.0		Light	7	2
Bread	31.0		Medium	7	7
Fish	22.5		Medium	7	2
Albumen	26.0		Dark	7	3

B. *Hyla.* Experiment started Apr. 17, 1911

	Length in mm.			Number of tadpoles	
Food	May 8	June 3	Color	Apr. 17	June 3
Liver	25	37	Dark	4	3
White beans	22	35	Medium	5	4
Brown beans	21	40	Medium	5	5
Suet	14	16	Dark	5	4

C. *Hyla.* Experiment started Apr. 17, 1911

	Length in mm.			Number of tadpoles
Food	Apr. 22	May 8	Color	Apr. 17
Egg	13	22	Light	4
White beans	13	20	Medium	5
Brown beans	11	22	Medium	5
Suet	11	14	Dark	5

To see if it would be possible to lighten the color of tadpoles that were already strongly pigmented, some very dark tadpoles collected from a pond were fed upon yolk of egg. In nine days they were distinctly lighter than tadpoles from the same source that had been kept in the aquarium on a mixed diet. I do not regard this as a disappearance of pigment already present in the tadpole, but rather as a decrease in pigment production relative to growth. The proportion of pigment formed is less with egg yolk as food, so that the ratio of pigment to body size decreases, until within nine days, the difference in color is noticeable.

If we assume an oxidase reaction as the basis of pigment formation in the tadpoles we explain a decrease in the rate of

pigment formation by a decrease in the amount or power of the oxidase or by a decrease in the amount of the chromogen or by the presence of something which inhibits the action of the oxidase.

The oxidase in these experiments was certainly not administered to the animal directly, since all of the foods were boiled before being given, and oxidases are destroyed at this temperature. Therefore the oxidase was produced by the organism. If the difference in pigmentation was due to a greater amount of oxidase, the later could have been furnished only indirectly by the foods.

In considering the amount of chromogen contributed by the foods, one must consider their proteid content, since tyrosin, a common chromogen, is a decomposition product of the digested proteids. A study of the analyses of the various foods shows that the pigmentation is not correlated with the amount of proteid, since egg yolk which produced little pigment contains a large percentage of proteid, larger than beans, which produced more pigment. From the table it will be seen that while pigmentation may depend upon the kind of proteid fed, it cannot depend upon the gross amount of proteid (table 4). A few tabulations of the cleavage products of these foods are available (see table 10). It is notable that in these ov-albumen shows a larger percentage (2.4%) of tyrosin than does vitellin (1.6%). The differences are very slight, but it will be remembered that the differences in pigmentation are also small, and that tyrosin is so slightly soluble in water that artificial melanins are formed with very dilute solutions of the chromogen.

TABLE 4

Analyses of the foods used in experiments, from Hammarsten, "A Text Book of Physiological Chemistry," trans. by Mandel (1911, p.882–3).

	1000 parts contain						Relation of 1:2:3		
	1	2	3	4	5	6	1	:2	:3
	Proteids and extractives	Fat	Carbohydrates	Ash	Water	Waste			
Beef liver	196	56	11	17	720	....	100	28	0
Egg yolk	160	307	....	13	520	....	100	192	0
Egg albumen	103	7	7	8	875	....	100	7	7
Beans	27	1	66	6	888	12	100	4	244

It is quite possible that the two causes, perhaps three, always operate to some degree, that a strong-pigment forming food such as liver may furnish in the digestive process a large proportion of tyrosin or some other chromogen, and at the same time furnish few inhibiting factors. The third factor, not so easily accessible to experiment, may be an increased formation of the oxidase by a strong pigment-forming food.

The large proportion of fat in egg yolk suggested that the lecithin of the yolk might be the element that in some way brought about a decrease in pigment production. The results of Danilewsky supported the suggestion that lecithin might be an inhibitor, possibly the only one.

Danilewsky (1895) placed tadpoles in a solution containing one part of lecithin to 15,000 parts of water. Other tadpoles were kept in water alone to serve as a control. The former became three times heavier and nearly twice as long as the corresponding controls. He thought the effect was due to the stimulating effect of the lecithin rather than to any great amount of nourishment contained in it. He adds: "Il faut encore noter que tous les têtards *lècithiniques* étaient beaucoup moins pigmentés que les larves de contrôle." He found also that when lecithin is injected into young rabbits or dogs there is a marked increase in their growth.

Miss King (1907) conducted a series of feeding experiments with large numbers of toad tadpoles. She refers to an apparent stimulating effect of lecithin in egg yolk and mentions meat as a good pigment producer.

Goldfarb (1910, p. 272) reviews the results of these and other experiments with lecithin and reports upon similar investigations of his own. He says, "Frog and toad tadpoles were placed in graded lecithin solutions ranging from one part of lecithin in 20,000 of water to toxic solutions of $\frac{1}{50}$ and kept therein throughout their period of metamorphosis (33 to 51 days). Other conditions, such as temperature, amount of solution, number of tadpoles in each dish, food, etc., were constant for each series. The control tadpoles showed at the end of the experiment a variation of 9 to 53 per cent in weight, 3 to 44 per cent in length. About 1,000 tadpoles kept in lecithin solutions showed a maxi-

mum variation of 23 to 64 per cent for the same period of time. There was no definite increase in size or weight in the increasing concentrations of lecithin, nor was there a definite gain among those in lecithin taken as a whole as contrasted with the controls."

These facts led to farther investigation of lecithin, its effect both upon the tyrosinase reaction and pigmentation in the larvae.

E. EFFECT OF LECITHIN AND VARIOUS FOODS USED IN EXPERIMENTATION, UPON THE TYROSINASE REACTION

The following tests *in vitro* of the effect of the various foods upon the tyrosinase reaction support the suggestion that the lecithin in egg yolk inhibits pigment formation.

Tyrosinase for the tests was obtained from different sources as follows:

(1) Fly larvae from six to ten days old were washed, chloroformed, and then ground with distilled water in a glass mortar. The aqueous extract thus obtained was filtered through glass or cotton wool, and used immediately. This solution is a very powerful one and turns orange pink throughout before one can get it measured into the test tubes.

(2) Meal worms were extracted in the same way and the course of the reaction is much the same, but the solution does not color quite as rapidly as in the case of the fly larvae.

(3) Mushrooms were extracted with glycerine and water, after having been ground in a glass mortar. The extract was filtered through ordinary filter papers.

(4) Potatoes were scraped and extracted with water for about an hour. This extract was filtered through filter papers and used as soon as possible. The solution is a pale orange pink by the time it is measured out into the test tubes.

A saturated solution of tyrosin in water was usually added to these solutions for the experiments, but the extracts already contained a chromogen since all of them darken after standing for half an hour. Since solutions color up in the same way when tyrosin is added as when it is not added, it seems likely that tyrosin is the chromogen already present in the solution. The extract from fly larvae gives a positive result for tyrosin when

tested with Million's reagent. Owing to the fact that the tyrosinase when isolated by precipitation with alcohol or other agents, is much less powerful than the original extract, in most of these experiments no attempt was made to isolate the oxidase. Kastle (1910, p. 63) has experienced the same difficulty and says, "Inasmuch as we have no criterion for judging of the absolute purity of a ferment, it is very doubtful whether much is gained by the attempt to isolate laccase and the other oxidases in pure condition."

Two series of experiments were made. In the first, the various foods under investigation were cooked and ground and then added to solutions of tyrosin and tyrosinase; in the second the foods were digested in pancreatin and pepsin and the filtrates used.

Series A. Undigested Foods

For these experiments 0.2 gm. of the food was weighed out after it had been thoroughly cooked by boiling. This portion was ground in a glass mortar with 10 cc. of distilled water and added to the tyrosinase solution with or without tyrosin. The results are more or less variable, but certain facts may be stated with assurance to hold for all sorts of tyrosinase used.

Albumen inhibits the action of the tyrosinase the least of any of the foods. Yolk and liver inhibit the reaction more than albumen—liver usually inhibiting more than yolk. Liver allowed to spoil and then cooked inhibits the reaction completely, giving a white precipitate and a clear, colorless liquid. Liver that has been kept for several days, but cooked from time to time to prevent its putrefaction, inhibits the reaction less than does the fresh liver. Fresh and stale eggs inhibit the reaction equally. Lecithin* inhibits the action of the tyrosinase markedly—the color appearing slowly and only toward the surface of the liquid.

* Lecithin was prepared as follows: Yolks of hen's eggs were washed in water without breaking the membrane. An equal volume of 10 per cent sodium chloride solution was added and the mixture extracted in a separatory funnel with two volumes of ether. To the ether fraction was added an equal volume of acetone. The precipitated lecithin was dried in a sulphuric acid dessicator.

Pepsin and pancreatin (Merck in both cases) were tested in the same way, 0.2 grams being ground in 10 cubic centimeters of water and the tyrosinase solution added. Pepsin inhibits the reaction markedly, sometimes entirely. The pancreatin tubes, on the other hand, are usually as dark as the control.

Although, in these tests, liver inhibits the reaction more than egg yolk, the result is reversed when the foods are digested, digestion apparently lessening the inhibitory action of the liver. As one would expect, whatever effects the foods may have on the reaction before digestion, these effects are more or less changed after digestion.

Series B. Digested Foods

In these experiments the foods were digested with pepsin and pancreatin and the filtrates added to the tyrosinase solution. In each case five grams of the food were ground in a glass mortar with ten cubic centimeters of distilled water, and digested with 0.6 gram of pepsin or pancreatin. A few drops of toluol were added and the tubes were kept in a warm place. After digesting for forty-eight hours, the masses were filtered. The tyrosin and tyrosinase were mixed and the solution measured out from a burette into test tubes containing a few drops of toluol and seven drops of filtrate or, in the case of the control, seven drops of distilled water.

By the time the solutions have been introduced into the tubes containing the filtrates and toluol and the tubes arranged for inspection they are all a delicate orange pink. The yolk tubes soon become paler, passing into a pinkish white and the pancreatins soon lose the pink tinge entirely, passing into a light greenish brown, at the same time turning a smoky black at the surface. This black color gradually deepens until the solution is jet black throughout. If after the reaction has gone on for twelve hours, the tubes are shaken, the three are all very dark, but the yolk tube is brown or greenish brown while the liver and albumen tubes are jet black.

The pepsin tubes go through the reaction more slowly, showing much of the orange pink color after the pancreatin tubes have lost their pink color and have become black at the surface.

The darkening toward the surface proceeds more slowly also showing more of the red and mahogany tints before reaching black. The solutions become as dark as the others if left long enough, and when shaken show the same slight difference between the yolk and the liver and albumen. Liver and albumen tubes are often the same shade, but if there is a difference, the albumen tube is usually darker. The control tube acts more like pepsin than pancreatin, retaining its pink color for some time as the pepsin filtrates do.

The more rapid formation of color in the pancreatin tubes as compared with the pepsin or control tubes is, I think, due in part to the fact that the filtrates contain products of digestion, among which are probably some which serve as chromogens. Tyrosin is present among the cleavage products of most foods; and there may be other chromogens present. Their presence would account for the fact that the test tubes containing pancreatin filtrates color more quickly than the control tubes do. The tubes containing pepsin filtrates, on the other hand, probably contain enough pepsin to slow down the reaction, since we found that pepsin alone inhibits the reaction markedly. It is also possible that they contain less chromogen than the pancreatin filtrates. Probably both factors operate to produce the result, a color reaction which generally runs parallel with that of the control tubes.

Gessard (1901) obtained a similar result when he found that forty drops of blood serum from a calf retarded the tyrosinase reaction nine days, while fifty drops of water retarded it for a month. It is highly probable that some chromogen was present in the blood serum which would at least contribute more toward pigment formation than would any elements contained in an equal amount of water.

Though the results of the experiments are not altogether constant, the variability in the reaction is probably to be accounted for partly by the fact that different eggs and livers were used in different experiments, partly by the fact that the foods may have reached different stages of digestion in the different sets of experiments, and perhaps by variability of other and unknown factors. In spite of these differences, however, the experiments

show plainly that lecithin and egg yolk inhibit to some extent the action of certain tyrosinases of vegetable and animal origin. This being so, what will be the effect when lecithin is fed to the tadpoles along with a food which produces marked pigmentation?

F. EFFECT OF LECITHIN UPON PIGMENTATION

Experiments were accordingly made to determine the effect of lecithin when it is fed along with a food that ordinarily produces considerable pigment. When lecithin was mixed with the food it was placed in the dishes every other day after the dishes had been cleaned and the food and water renewed. The amount of lecithin used was not weighed each time, but it probably varied between fifteen and twenty milligrams in weight. It dissolved after eight or ten hours.

Of two lots of *Rana* tadpoles, one was fed albumen and the other albumen and lecithin. Following are the notes on the experiments. Table 5 shows the length measurements on different dates.

TABLE 5

Length measurements of *Rana* tadpoles fed on albumen and albumen plus lecithin. Length measurements represent average length of all the tadpoles. Eight tadpoles in each lot.

Rana. Experiment started Feb. 6, 1912

	Length in mm.			
Food	Feb. 19	Feb. 26	Mar. 5	Mar. 25
Albumen	17.6	18.6	19.3	21.5
Albumen + lecithin	18.2	21.1	23.0	26.5

Feb. 21. Tadpoles fed on albumen plus lecithin are lighter than those fed on albumen alone. The difference is small but distinct.

Mar. 5. Tadpoles fed on albumen plus lecithin are very plainly lighter and larger than tadpoles fed on albumen.

Mar. 14. (Same as Mar. 5.)

Mar. 25. Color difference seen before is now scarcely noticeable. Size difference very plain.

Apr. 2. Color difference plain once more.

Apr. 10. On account of the size difference it is difficult to compare the two sets of tadpoles with accuracy. One tadpole fed on albumen plus lecithin is darker than the others but the rest are lighter than the albumen-fed tadpoles, showing a yellowish brown tinge rather than black.

The same experiment was carried out with *Hyla* tadpoles with the same results (table 6).

Table 6

Length measurements of *Hyla* tadpoles fed on albumen and albumen plus lecithin. Length measurements represent average length of all the tadpoles in the dish.

Hyla. Experiment started Feb. 21

	Length in mm.		
Food	Feb. 26	Mar. 5	Mar. 25
Albumen	12.5	17.1	22.0
Albumen + lecithin	12.3	16.9	25.6

Mar. 5. Tadpoles fed on lecithin plus albumen are distinctly lighter than the others. The tadpoles fed on albumen alone have slender, pinched bodies, while the others are the normal shape and size.

Mar. 25. The color difference is scarcely noticeable.

Apr. 10. Some tadpoles on lecithin plus albumen are as dark as those on albumen alone, but most of them are lighter.

Liver plus lecithin, and liver alone, were fed to two different sets of *Rana* tadpoles with the following results (table 7):

Table 7

Length measurements of *Rana* tadpoles fed on liver and liver plus lecithin. Length measurements represent average length of all the tadpoles. Eight tadpoles in each lot.

Rana. Experiment started Feb. 6, 1912

	Length in mm.			
Food	Feb. 20	Feb. 26	Mar. 6	Mar. 14
Liver	21.4	24.2	27.4	30.25
Liver + lecithin	20.6	24.05	28.2	30.29

Feb. 21. Tadpoles fed on liver alone are darker than the others.

Feb. 26. Tadpoles fed on liver alone are darker than the others.

Mar. 14. Some about the same color, others darker in dish containing liver alone.

The same experiments with *Hyla* gave the following results (table 8):

TABLE 8

Length measurements of *Hyla* tadpoles fed on liver and liver plus lecithin. Length measurement represents average length of all the tadpoles. Six tadpoles in each lot.

Hyla. 1912

	Length in mm.	
Food	Mar. 5	Mar. 14
Liver	19.5	24.4
Liver + lecithin	19.6	26.2

Mar. 14. Tadpoles fed on liver plus lecithin are lightest—have a greenish tinge while others are black.

Mar. 25. Tadpoles fed on liver are all dead.

Two sets of *Hyla* tadpoles were fed on egg yolk and egg yolk plus lecithin (table 9):

TABLE 9

Length measurements of tadpoles fed on yolk and yolk plus lecithin. Length measurements represent average length of all the tadpoles. Eight tadpoles in each lot.

Hyla. 1912

	Length in mm.		
Food	Mar. 5	Mar. 14	Mar. 25
Yolk	15.7	18.2	22.6
Yolk + lecithin	15.6	17.6	22.1

Mar. 14. Sizes are uneven. No marked color differences. A few lighter individuals among the tadpoles fed on yolk.

Apr. 1. Tadpoles fed on yolk average slightly darker than the others—pigmentation very uneven.
(Tadpoles accidentally mixed, experiment discontinued.)

The experiments plainly show that lecithin lightens the color of the tadpoles. It is not clear that lecithin plus yolk of egg produces lighter colored tadpoles than yolk alone does. It would appear that for tadpoles of the size reached by these at least, additional amounts of lecithin do not lighten the tadpoles noticeably.

Miss King (1907) has suggested that the tadpoles that are fed with lecithin are not so thrifty as the others. Although there has been a slightly larger percentage of deaths among the tad-

poles fed on yolk of egg than among those fed on liver, the tadpoles on lecithin mixed with other foods show a smaller percentage of deaths than the control lots receiving no lecithin.

It has been noticed in the experiments with lecithin in connection with other foods, that the color differences vary from time to time. Such differences have been noticed in all the experiments to a greater or less extent. In general the difference between the color of tadpoles fed on yolk and those fed on liver is very noticeable at the end of the first week and continues to be very marked until the larvae are about half grown, when it becomes less distinct. From about the time the hind limbs appear until the metamorphosis is complete, the color difference is again marked.

These differences are never great enough to suggest an actual disappearance of pigment already formed, but rather a slight difference in the rate of pigment production at different stages of development. That is, the pigment production in tadpoles fed on egg yolk or lecithin though at all times less than in the tadpoles fed on liver may be greater at one time than at another. It is possible that the tadpole at different stages of development is differently influenced by the lecithin. The differences may be more or less periodic, but more observations and histological data are necessary for an intelligent discussion of this phase of the problem.

G. Effect of certain other organic substances upon the tyrosinase reaction and upon pigmentation

A consideration of the effect of various other chemicals upon the tyrosinase reaction is important if we grant that chemical substances thus profoundly influence pigment formation.

Abderhalden and Guggenheim (1907) found that n/100 hydrochloric acid inhibits the action of tyrosinase and n/100 sodium hydroxide retards it considerably. Neutralization of acid or alkali fail to restore the original activity of the oxidase.

Chodat and Staub (1907) observe that the oxidation of tyrosin by tyrosinase is diminished by glycin, leucin, and alanin. They find that tyrosin acts upon certain peptids such as tyrosin

anhydride and glycyl-tyrosin anhydride, giving rise to yellow substances which do not become black as does tyrosin itself. However, a mixture a glycyl-tyrosin anhydride with glycin gives with tyrosinase a rose color changing to bluish green, with alanin it gives a deep red, and with leucin a deep brown color.

Abderhalden and Guggenheim (1907) studied the action of tyrosinase from *Russula delica* on tyrosin and various tyrosin-containing polypeptids. Aspartic and glutaminic acids and other amino acids inhibited the action, especially if they were present in strong solution. Polypeptids containing tyrosin residues were colored by tyrosinase, the color being somewhat modified by the nature of the amino acid combined with the tyrosin in the polypeptid. They conclude that the character of the pigment resulting from the *action of tyrosinase on tyrosin is dependent upon the combination in which the tyrosin exists.*

TABLE 10

Cleavage products of certain animal and vegetable proteids; ov-albumin, vitellin, and gliadin taken from Hammarsten (1911), gluten from Plimmer (1908).

	Ov-albumin[1]	Vitellin[4]	Gliadin		Gluten, from wheat[7]
			a^5	b^6	
Glycocoll	0.0	1.1	0.02	0.9	0.4
Alanine	2.1	+	2.0	2.66	0.3
Valine	.... } 17[2]	2.4	0.21	0.33	....
Leucine	6.1 }	11.0	5.61	6.00	4.1
Serine	1.1	....	0.13	0.12	....
Aspartic Acid	1.5	0.5	0.5	1.24	0.7
Glutamic Acid	8.0	12.2	37.33	31.5	24.0
Cystin	0.3[3]	....	0.45	.....	....
Phenylalanine	4.4	2.8	2.35	2.6	1.0
Tyrosine	2.4[3]	1.6	1.20	2.37	1.9
Proline	2.25	3.3	7.06	2.4	4.0
Oxyproline	....	....	.....	.....	....
Tryptophane	....	....	+	1.0	+
Histidine	....	....	0.61	1.7	1.2
Arginine	....	....	3.16	3.4	4.4
Lysine	....	....	0.0	0.0	2.2
Ammonia	....	....	5.11	.....	2.5

[1] Abderhalden and Pregl (1905).
[2] Levene and Beatty (1907).
[3] K. Mörner (1901).
[4] Abderhalden and Hunter (1906).
[5] Osborne and Clapp (1906).
[6] Abderhalden and Samuely (1905), and Abderhalden (1909).
[7] Abderhalden and Malengreau; Kossel and Kutscher.

In the analyses of various cleavage products, table 10, gliadin and gluten are notable for their high percentage of glutamic acid. Glutamic acid is noted by Abderhalden and Guggenheim as an inhibitor of the tyrosinase reaction when tyrosinase from *Russula delica* is used. Accordingly gliadin and gluten (made from white flour, dried, ground, and fed in powdered form) were fed to different sets of tadpoles. These foods produce so little growth that the results are very inconclusive.

The results with liver, yolk and gliadin are as follows (table 11):

Table 11

Length measurements of *Hyla* tadpoles fed on liver, yolk, and gliadin. Length measurements represent average length of all the tadpoles in a dish.

Hyla. Experiment started Feb. 24, 1912

	Mar. 5		Mar. 25	
Food	Length in mm.	Number of tadpoles	Length in mm.	Number of tadpoles
Liver	15.8	18	.....	0
Yolk	15.3	18	28.0	14
Gliadin	12.5	18	15.0	15

Mar. 5. Liver-fed tadpoles black. Gliadin-fed tadpoles dark, but not so dark as liver, yolk-fed tadpoles lighter with a few very light ones.

Mar. 14. Liver-fed tadpoles all black; yolk-fed tadpoles—four very light, the rest medium; gliadin, one light, the rest medium.

Of three sets of *Rana* tadpoles one was fed on raw flour, one on gluten, and the third on gliadin. Here again the growth was so slight that the experiment was unsatisfactory (table 12):

Table 12

Length measurements of *Rana* tadpoles fed on flour, gluten, and gliadin. Length measurements represent the average length of all the tadpoles. Equal number of tadpoles at the beginning of the experiment.

Rana. Experiment started Feb. 24, 1912

	Length in mm.		Number of tadpoles
Feed	Mar. 6	Mar. 25	May 6
Flour	15.7	19.1	9
Gluten	15.8	18.5	1
Gliadin	15.7	.....	....

Mar. 25. No noticeable color difference.

Apr. 10. Only one gluten-fed tadpole left. This one is larger and slightly darker than the average of the flour-fed tadpoles.

The same experiment with *Hyla* tadpoles gave the following data (table 13):

TABLE 13

Length measurements of *Hyla* tadpoles fed on flour, gluten, and gliadin. Length measurements represent the average length of all the tadpoles in a dish.

Hyla. Experiment started Feb. 24, 1912

	Length in mm.	
Food	Mar. 6	Mar. 24
Flour	13.0	18.3
Gluten	13.3	19.6
Gliadin	12.2	13.7

Mar. 24. Tadpoles all nearly the same color,—if any difference gluten-fed are darkest, gliadin-fed lightest.

Gortner (1911b) finds that orcin, resorcin, and phloroglucin inhibit the action of tyrosinase extracted from potatoes, meal worms, and the periodical cicada. He says: "It would appear from these data, that aromatic compounds which carry two hydroxyl groups in meta position to each other may act as chemical anti-oxidases on tyrosinase, and completely inhibit its action. Other oxidases are not inhibited, but are able to oxidize these same m-dihydroxl compounds, forming colored bodies of an unknown nature."

Phloroglucin and resorcin were mixed with liver and fed to *Hyla* tadpoles. The amounts were not weighed, but about fifteen milligrams was rubbed up with the liver and put into the dish. The tadpoles on resorcin did not thrive, most of them died very soon (table 14):

TABLE 14

Length measurements of tadpoles fed on liver, liver + resorcin, and liver + phloroglucin. Measurements represent the average length of all the tadpoles in the dish.

Hyla. Experiment started Mar. 18, 1912

	Mar. 25		Apr. 11
Food	Length in mm.	Number of tadpoles	Number of tadpoles
Liver	14.1	6	6
Liver + resorcin	15.4	4	0
Liver + phloroglucin	14.3	6	4

Mar. 25. All tadpoles the same color.

Apr. 1. All tadpoles the same color.

Apr. 11. Of the four remaining tadpoles on liver plus phloroglucin, two are as dark as the six tadpoles fed on liver alone, and two are slightly lighter.

The same experiment with albumen as food gives the following results (table 15):

Table 15

Length measurements of tadpoles fed on albumen, albumen + resorcin, and albumen + phloroglucin. Measurements represent the average length of all the tadpoles in the dish.

Hyla. Experiment started Mar. 18, 1912

Food	Length in mm. Mar. 25
Albumen	13.6
Albumen + resorcin	13.1
Albumen + phloroglucin	12.8

Mar. 25. Tadpoles fed on albumen plus phloroglucin are very slightly lighter than the other two sets, which are both the same color.

Apr. 11. Tadpoles fed on albumen plus phloroglucin are very slightly lighter than those on albumen, but the difference is scarcely noticeable.

This group of experiments, as will be noted, was tried but once and with a small number of tadpoles, so they can be regarded only as a beginning in this direction. The results indicate that the various substances may affect the color of the tadpoles to some extent.

H. HISTOLOGICAL DIFFERENCES BETWEEN CHROMATOPHORES OF LARVAE FED UPON DIFFERENT FOODS

The statements as to the color differences in the tadpoles have been made thus far on the basis of their appearance to the unaided eye. The differences as shown by the microscope are no less marked and show plainly that there is actually less pigment in the egg-fed tadpoles (plate 1).

With the low powers of the microscope the black epidermal chromatophores of the dark *Rana* tadpoles appear to be greatly branched, and so filled with pigment that they come very close

together, while in the light egg-fed tadpoles, the chromatophores, though perhaps not less numerous are more slender and delicate and very little branched. In very light specimens the pigment is in spots that are scarcely elongated at all (pl. 1, figs. 5–8).

The form of the chromatophores in the *Hyla* is somewhat different. The body of the chromatophore is not so long, but the branching processes are longer and finer and in dark individuals form a close network of fine interlacing branches (pl. 1, figs. 3 and 4). Between the two extremes in both species are various grades of difference, so that the chromatophores of an unusually dark egg-fed tadpole may not differ greatly from those of a lighter colored liver-fed individual.

A study of sections shows that the chromatophores of the dark tadpoles are larger because they contain many more of the brown melanin granules. These granules are so numerous that the pigment forms a continuous network in the intercellular spaces, while in the light tadpoles the amount of melanin is so much less that the pigment masses appear as small spots with few or no processes. Camera drawings of the typical chromatophores of the two sorts make this difference clear.

Fig. 1

Fig. 2

Sections of epidermis of larvae of *Rana* sp. × 450. (Drawn with aid of camera lucida.)

Fig. A. Tadpole fed on yolk of egg.

Fig. B. Tadpole fed on liver.

I. EFFECT OF CHANGES IN LIGHT, HEAT, AND FOOD UPON PIGMENTATION

To determine the influence of light and heat upon the color differences produced in the tadpoles by different foods, the following experiment was carried out. Eight dishes of tadpoles, all from the same bunch of eggs, were arranged as shown below.

Warm:
In constant temperature, box (of glass) kept at about 26.5 C.
- In *dark.* (in black pasteboard box)
  - *a.* fed on liver
  - *b.* fed on yolk
- In *light.*
  - *c.* fed on liver
  - *d.* fed on yolk

Cold:
In north basement room. (The temperature of this room varied very little and was always considerably below ordinary room temperature.)
- In *dark.* (in black pasteboard box)
  - *e.* fed on liver
  - *f.* fed on yolk
- In *light.*
  - *g.* fed on liver
  - *h.* fed on yolk

Table 16

Length measurements of *Rana* tadpoles under different conditions of light, temperature, and food. Measurements are average length of all the tadpoles in a dish. Experiment began with eight tadpoles in each lot.

Rana. Experiment started Feb. 10, 1912

Conditions of the experiment			March 5	
Temperature	Lighting	Food	Length in mm.	Number living
Warm	Dark	Liver	28.0	3
Warm	Dark	Egg yolk	27.5	5
Warm	Light	Liver	31.4	4
Warm	Light	Egg yolk	26.5	2
Cold	Dark	Liver	19.3	8
Cold	Dark	Egg yolk	20.8	8
Cold	Light	Liver	21.2	8
Cold	Light	Egg yolk	20.3	8
AVERAGES				
Cold			20.4	32
Warm			28.6	14
	Light		23.2	22
	Dark		23.0	24
		Egg yolk	22.6	23
		Liver	23.2	23

The series of colors is the same under the different conditions of temperature. In both cases the series from darkest to lightest coloring is as follows:

Darkest tadpoles—Those fed upon liver and kept in the light.
Those fed upon egg and kept in the light.
Those fed upon liver and kept in the dark.
Lightest tadpoles—Those fed upon egg and kept in the dark.

It is plain from this experiment that tadpoles raised in the light are darker than those raised in the dark and that tadpoles fed upon liver and kept either in the light or in the dark are darker than those fed upon egg under the same conditions. The difference in size and development between the tadpoles kept at a high temperature and those in the low temperature are so great that the two series cannot well be compared, but no marked difference in color between the two series can be distinguished. It is evident that changes in both food and light influence the rate of pigment formation markedly and that light is a somewhat more potent factor than liver in increasing the rate of pigment production.

These conclusions as to increase of pigmentation in the light and increase in the rate of growth at a higher temperature confirm results already reported (table 16). The average length measurements of all tadpoles kept in the dark compared with those kept in the light are interesting in view of the conflicting statements that have been made by various observers as to the comparative rate of growth in the dark and in the light. These figures support the contention that there is very little if any difference between the amount of growth in the light and in the dark.

J. SUMMARY

A consideration of Weismann's theory, the factor hypothesis, and the results of chemical research, leads one, it seems to me, to see in the last two named the greatest hope for the solution of problems of color differentiation. The difficulties and complications are great, but the field for research is correspondingly large and fruitful.

The present research is by no means complete, the results so far attained suggesting numerous very pertinent points that should be investigated farther. It does, however, furnish certain definite facts which it is hoped will add something to current conceptions of color differentiation.

The research shows that pigment in *Rana* and *Hyla* tadpoles is not correlated with amount of nutrition, as claimed by Tornier for *Pelobates* larvae, but, as suggested by instances cited by Darwin and Wallace, is dependent rather upon substances specific for color in the nutritive material. These substances may bring about a change in the amount of pigment-forming substances produced or slightly alter the character or combination of these substances and thus change the amount or color of the pigment.

The fact is made clear that lecithin acts as a partial inhibitor of the tyrosinase reaction in the test tube, and when it is fed to tadpoles, pigment formation is checked to a noticeable degree, indicating that inhibitors or modifiers of the pigment formation may be introduced into the organism with the food.

The similarity of the effect of lecithin in the test tube and in the body of the tadpole makes it probable that the tyrosinase reaction or a similar oxidase reaction is the basis of pigment formation in the tadpole.

BIBLIOGRAPHY

Abderhalden, E., and Guggenheim, M.
1907. Versuche über die Wirkung der Tyrosinase aus *Russula delica* auf Tyrosin, tyrosinhaltige Polypeptide und einige andere Verbindungen unter verschiedenen Bedingungen. Zeit. f. physiol. Chem., 54, 331–353.

Abderhalden, E., and Hunter, A.
1906. Hydrolyse des im Eigelb des Hühnereies enthaltenen Proteins (''Vitellin''). Zeit. physiol. Chem., 48, 505–512.

Abderhalden, E., and Pregl, F.
1905. Die Monoaminosäuren des krystallisierten Eieralbumins. Zeit. physiol. Chem., 46, 24–30.

Abderhalden, E., and Samuely, F.
1905. Die Zusammensetzung des ''Gliadins'' des Weizenmehles. Zeit. physiol. Chem., 44, 276–283.

Bertrand, G.
1908. Recherches sur la mélanogénèse: Action de la tyrosinase sur la tyrosine. Ann. Inst. Pasteur, **22**, 381–389.

Castle, W. E.
1907. On a case of reversion induced by cross-breeding and its fixation. Sci., n.s., **25**, 151–153.

Castle, W. E., in collaboration with H. E. Walter, R. C. Mullenix, and S. Cobb.
1909. Studies of inheritance in rabbits. Publ. Carnegie Inst., Washington, no. 114, pp. 69, 4 pls., 4 figs. in text.

Chodat, R., and Staub, W.
1907. Nouvelles recherches sur les ferments oxydants. III, La spécificite de la tyrosinase et son action sur les produits de la dégradation des corps protéiques. Arch. Sci. Phys. (4), Genève, **24**, 172–191.

Danilewsky, B.
1895. De l'influence de la lécithine sur la croissance et la multiplication des organismes. C.-R. Acad. Sci., Paris, **121**, 1167–1170.

Darwin, C.
1868. The variation of animals and plants under domestication. Authorized ed., with a preface by Prof. Asa Gray. (New York, Orange Judd & Co.), vol. i, x + 494, 43 figs. in text, vol. ii, viii + 568.

Dewitz, I.
1902. Recherches expérimentales sur la métamorphose des insectes. C.-R. Soc. Biol., Paris, **54**, 44–45.

Gessard, C.
1901. Études sur la tyrosinase. Ann. Inst. Pasteur, **15**, pp. 593–614.

Goldfarb, A. J.
1910. Does lecithin influence growth? Arch. f. Entwicklungsmechanik, **29**, 255–274.

Gortner, R. A.
1910a. The origin of the brown pigment in the integuments of the larva of *Tenebrio molitor*. Journ. Biol. Chem., **7**, 365–370.
1910b. Spiegler's "white melanin" as related to dominant or recessive white. Amer. Nat., **44**, 497–502.
1911a. Studies on melanin. II, The pigmentation of the adult periodical cicada (*Tibicen septendecim* L.). Journ. Biol. Chem., **10**, 89–94, 1 pl.
1911b. Studies on melanin. III, The inhibitory action of certain phenolic substances upon tyrosinase. Journ. Biol. Chem., **10**, 113–122.
1911c. Studies on melanin. IV, The origin of the pigment and the color pattern in the elytra of the Colorado potato beetle (*Leptinotarsa decimlineata* Say). Amer. Nat., **45**, 743–755.
1911d. On melanin. Biochem. Bull., **1**, 207–215.

Hammarsten, Olaf.
1911. A text-book of physiological chemistry. Authorized translation by John A. Mandel. (New York, Wiley), viii + 964 pp., 1 pl., 3 tables.

Kastle, J. H.
1909. The oxidases and other oxygen-catalysts concerned in biological oxidations. Pub. Health and Marine-Hospital Service, U. S., Hyg. Lab. Bull., no. 59, 164 pp.

King, H. D.
1907. Food as a factor in the determination of sex in amphibians. Biol. Bull., **13**, 40–56.

Levene, P. A., and Beatty, W. A.
1907. Ueber die analyse der Spaltungsprodukte des Eialbumins. Biochem. Zeit., **4**, 305–311.

Morner, K. A. H.
1901. Zur Kenntniss der Bindung des Schwefels in den Proteinstoffen. Zeit. physiol. Chem., **34**, 207–338.

Osborne, T. B., and Clapp, S. H.
1906. The chemistry of the protein bodies of the wheat kernel. Part III. Am. Jour. Physiol., **17**, 231–265.

Phisalix, C.
1905. Sur le changement de coloration des larves de *Phyllodromia germanica*. C.R. Soc. Biol., Paris, **59**, 17–18.

Plimmer, R. H. A.
1908. The chemical constitution of the proteins. (London, Longmans), vol. i, xii + 100 pp., vol. ii, xi + 66 pp.

Powers, J. H.
1908. Morphological variation and its causes in *Amblystoma tigrinum*. Studies from Zool. Lab. Univ. Nebraska, **71**, 77, 9 pls.

Riddle, O.
1908. The genesis of fault-bars in feathers and the cause of alternation of light and dark fundamental bars. Biol. Bull., **14**, 328–370, 4 pls., 5 figs. in text.
1909. Our knowledge of melanin formation and its bearing on the Mendelian description of heredity. Biol. Bull, **16**, 316–351.

Romanes, G. J.
1895. Darwin, and after Darwin. An exposition of the Darwinian theory and a discussion of post-Darwinian questions. II, Post-Darwinian questions, heredity and utility. (Chicago, Open Court), x + 344, 1 pl., 4 figs. in text.

Roques, X.
1909. Sur la variation d'une enzyme oxydante pendant la métamorphose chez un Trichoptère (*Limnophilus flavicornis* Fabr.). C.-R. Acad. Sci., Paris, **149**, 418–419.

Tornier, G.
1907. Nachweis über das Entstehen von Albinismus, Melanismus und Neotenie bei Fröschen. Zool. Anz., **32**, 284–288.
1908. Vorläufiges über experimentell erzielten Hautalbinismus bei Axolotl-larven. Berlin, Sitz Ber. Ges. nat. Freunde, **1908**, 66–67.

EXPLANATION OF PLATE 1

Fig. 1. *Rana* sp. The lighter tadpole was fed upon yolk of egg, the darker one was fed upon liver. From photograph, natural size.

Fig. 2. *Hyla regilla.* The lighter tadpole was fed upon yolk of egg, the darker one was fed upon liver. From photograph, natural size.

Figs. 3–8. Epidermal chromatophores of amphibian larvae. From photographs, magnified about forty-five diameters.

Fig. 3. *Hyla regilla.* Tadpole fed on liver.

Fig. 4. *Hyla regilla.* Tadpole fed on yolk of egg.

Fig. 5. *Rana* sp. Chromatophores of tail region, tadpole fed on liver.

Fig. 6. *Rana* sp. Chromatophores of tail region, tadpole fed on yolk of egg.

Fig. 7. *Rana* sp. Chromatophores of body of larva, tadpole fed on liver.

Fig. 8. *Rana* sp. Chromatophores of body of larva, tadpole fed on yolk of egg.

1

2

3

4

5

6

7

8

OCKAYNE—BOSTON

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY

Vol. 11, No. 5, pp. 89-126, pl. 2 June 21, 1913

SAGITTA CALIFORNICA, N. SP., FROM THE SAN DIEGO REGION

INCLUDING REMARKS ON ITS VARIATION AND DISTRIBUTION

BY

ELLIS L. MICHAEL

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY

UNIVERSITY OF CALIFORNIA PUBLICATIONS

Note.—The University of California Publications are offered in exchange for the publications of learned societies and institutions, universities and libraries. Complete lists of all the publications of the University will be sent upon request. For sample copies, lists of publications or other information, address the Manager of the University Press, Berkeley, California, U. S. A. All matter sent in exchange should be addressed to The Exchange Department, University Library, Berkeley, California, U. S. A.

OTTO HARRASSOWITZ, LEIPZIG.

Agent for the series in American Archæology and Ethnology, Classical Philology, Education, Modern Philology, Philosophy, Psychology, History.

R. FRIEDLAENDER & SOHN, BERLIN.

Agent for the series in American Archæology and Ethnology, Botany, Geology, Mathematics, Pathology, Physiology, Zoology, and Memoirs.

ZOOLOGY.—W. E. Ritter and C. A. Kofoid, Editors. Price per volume $3.50. Commencing with Volume II, this series contains Contributions from the Laboratory of the Marine Biological Association of San Diego.

Cited as Univ. Calif. Publ. Zool.

Volume 1, 1902-1905, 317 pages, with 28 plates $3.50

Volume 2 (Contributions from the Laboratory of the Marine Biological Association of San Diego), 1904-1906, xvii + 382 pages, with 19 plates $3.50

Volume 3, 1906-1907, 383 pages, with 23 plates $3.50

Volume 4, 1907-1908, 400 pages, with 24 plates $3.50

A list of titles in volumes 1-4 will be sent on request.

Vol. 5. (Contributions from the Museum of Vertebrate Zoology.)

1. The Biota of the San Bernardino Mountains, by Joseph Grinnell. Pp. 1-170, plates 1-24. December, 1908 ..... 2.00
2. Birds and Mammals of the 1907 Alexander Expedition to Southeastern Alaska, by Joseph Grinnell and others. Pp. 171-264, pls. 25-26, figs. 1-4. February, 1909 ..... .75
3. Three New Song Sparrows from California, by Joseph Grinnell. Pp. 265-269. April, 1909 ..... .05
4. A New Harvest Mouse from Petaluma, California, by Joseph Dixon. Pp. 271-273. August, 1909 ..... .05
5. A New Cowbird of the Genus *Molothrus*, with a note on the Probable Genetic Relationships of the North American Forms, by Joseph Grinnell. Pp. 275-281, 1 text figure. December, 1909 ..... .05
6. Two New Rodents from Nevada, by Walter P. Taylor. Pp. 283-302, plates 27-29.
7. A Northern Coast Form of the California Gray Fox, by Joseph Dixon. Pp. 303-305.

   Nos. 6 and 7 in one cover. February, 1910 ..... .20
8. Two Heretofore Unnamed Wrens of the Genus Thryomanes, by Joseph Grinnell. Pp. 307-309.
9. The Savannah Sparrow of the Great Basin, by Joseph Grinnell. Pp. 311-316.
10. A Second Record of the Spotted Bat (*Euderma maculatum*) for California, by Joseph Grinnell. Pp. 317-320, plate 30.

    Nos. 8, 9, and 10 in one cover. February, 1910 ..... .15
11. Mammals of the 1908 Alexander Alaska Expedition, with Descriptions of the Localities Visited and Notes on the Flora of the Prince William Sound Region, by Edmund Heller. Pp. 321-360, plates 31-32.
12. Birds of the 1908 Alexander Alaska Expedition, with a Note on the Avifaunal Relationships of the Prince William Sound District, by Joseph Grinnell. Pp. 361-428, plates 33-34, 9 text-figures.

    Nos. 11 and 12 in one cover. March, 1910 ..... $1.00

    Index, pp. 429-440.

Vol. 6. 1. (XXIII) On the Weight of Developing Eggs. Part I, The Possible Significance of Such Investigations, by William E. Ritter; Part II, Practicability of the Determinations, by Samuel E. Bailey. Pp. 1-10. October, 1908 ..... .10

2. (XXIV) The Leptomedusæ of the San Diego Region, by Harry Beal Torrey. Pp. 11-31, with text figures. February, 1909 ..... .20

---

* Roman numbers indicate sequence of the Contributions from the Laboratory of the Marine Biological Association of San Diego.

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY

Vol. 11, No. 5, pp. 89-126, pl. 2 June 21, 1913

SAGITTA CALIFORNICA, N. SP., FROM THE SAN DIEGO REGION

INCLUDING REMARKS ON ITS VARIATION AND DISTRIBUTION

BY

ELLIS L. MICHAEL

INTRODUCTION

After publishing the results of a long and critical study of the chaetognatha of the San Diego region involving the individual identification of nearly 80,000 specimens, a few net-hauls made in October, 1911, unexpectedly yielded what the former prolonged search failed to reveal—a new species. Popping, as it were, into existence so suddenly and being the only new chaetognath taken from California waters, this species has seemed to me to take appropriately the name, *Sagitta californica*.

While certain very apparent characteristics of this new species seemingly make it impossible to confuse it with any other, still it sometimes happens that specimens are described as constituting a new species when the differential characteristics upon which the definition is based later prove to be abnormalities or extremes of variability within an old species. I have endeavored to guard against such a pitfall by making accurate diagnostic measurements on as many specimens as practicable, and to this end table 1 is supplied, which is based upon micrometer measurements of fourteen structural features in each of one hundred of the most perfectly preserved specimens. In addition to this the

number of teeth and seizing jaws possessed by each individual, and the stage of maturity of ovary and seminal vesicle in each individual, are recorded. It is therefore hoped that the data in table 1 will materially aid future investigators in definitely settling questions of synonymy in the event of another similar species being discovered.

Again, much confusion occasionally arises because the *nature* as well as extremes of specific variation is not known, and its exposition constitutes one of the crying needs in the description of species. Pearl (1911, p. 110) has fully expressed this need as follows: "The systematist frankly makes no attempt whatever to describe or define a particular species as a species—in terms of its (the species) qualities. Instead he describes one individual animal belonging to this species; affirms either expressly or tacitly that all other individuals belonging to the species are "about" or "generally" like the individual described, and then he calls the net results the definition or description of the species. But now surely this is not a description of the species at all. An adequate description of the species will be one which takes account of its peculiarities as a unit, and indicates how it as a unit or as a whole is distinguished from other similar groups." Now the data compiled in table 1 afford an excellent opportunity for determining many of these important *specific* characteristics relative to variation and correlation in the several proportional measurements and number of teeth and seizing jaws. Therefore, following the customary description some space is devoted to this purpose. However, it is not my intention, had I the ability, to plunge the reader into the intricacies of biometrical analysis, though that might be desirable, but it is attempted so to arrange and analyze the data that all who read may readily comprehend.

DESCRIPTION

General Appearance.—To the naked eye *S. californica*, when placed in formalin upon a white background, assumes a very light yellowish-green color. It is palest about the neck and tip of tail, and shades gradually into a slightly deeper tint in the region of the ovaries. The brown seizing jaws, alone, stand out

conspicuously. On a black background the head, intestine, ventral ganglion, ovaries, and seminal vesicles appear much more opaque than the body proper which, like the tail, is translucent, nearly semi-opaque. The lateral fins, as well as tail-fin, are readily recognized as very transparent areas in decided contrast to the body. In degree of opacity *S. californica* resembles *S. serratodentata* more than any other species, although it is more translucent than is the latter.

The presence of numerous tactile hairs (pl. 2, fig. 1) extending from head to seminal vesicles, reveals, to the naked eye, a pronounced serrated appearance, especially between the head and ventral ganglion. These hairs occur most abundantly along the anterior half of the collarette. In older individuals, from four to twelve may be present on each of the paired fins and on the tail-fin. These hairs, like those in *S. bipunctata* and other species, are rendered much less conspicuous after long preservation in either alcohol or formalin.

Characters.—Body very firm and rigid, retaining its form almost perfectly. Neck and constriction at tail-septum prominent, but rendered inconspicuous by the collarette. Body slightly widest throughout middle third, tapering very gradually toward head and tail. Lateral fields small. Muscles thick and strong. Corona ciliata not observed.

Collarette (pl. 2, fig. 1), massive and very long, *extending from head to tail-septum, and thence to seminal vesicles.* Broadest just behind head (13–14 per cent of maximum body-width), gradually narrowing caudally until, opposite the posterior end of anterior fins, it is only about 3 per cent of the maximum body-width. From here it may vary slightly in width until it disappears at the tail-septum. Behind this structure, the collarette reappears and broadens regularly until it attains a width of about 12 per cent directly anterior of the seminal vesicles. It then very abruptly narrows, disappearing entirely at the vesicles.

Anterior fin shorter and narrower than posterior fin, varying in length from 16.5 to 21.8, and in width from 1.65 to 3.35 per cent of total length of animal. It approaches closely to but does not reach the ventral ganglion, the interval varying from 0.76

to 2.83 per cent of total length of animal. Form approximately triangular, the position of greatest width being opposite the rounded obtuse angle in the caudal fourth of the fin.

Posterior fin varies in length from 19.4 to 26.4, and in width from 2.96 to 5.27 per cent of total length of animal. It approaches but never reaches seminal vesicles, the interval varying from 2.19 to 4.60 per cent of total length of animal. More than 50 per cent of fin in front of tail-septum, the extremes of variation being 51 and 61 per cent. Position of greatest width about half way between tail-septum and posterior extremity of fin. Interval from anterior to posterior fin varies from 11.7 per cent of total length of animal in the younger individuals to 5.90 per cent in the older ones.

Vestibular ridge (pl. 2, fig. 2), provided with irregularly rounded papillae, so arranged that one papilla is usually opposite the interval between adjacent teeth. However, some intervals are skipped, so that the number of teeth is greater than the number of papillae, notwithstanding the fact that two or three papillae occur internally to the teeth. One tooth, sometimes two and rarely more, project beyond wing of ridge, the adjacent one usually being well covered by it. Notch covers the external four or five teeth. External process short and blunt, scarcely one and a half times longer than broad.

Anterior teeth (pl. 2, fig. 3), three to seven, usually five or six. They are closely set, with overlapping bases. Very divergent distally.

Posterior teeth (pl. 2, fig. 2), eight to sixteen, usually ten or eleven. They are closely set and overlapping, though less markedly than anterior teeth. Slightly divergent distally. While they are nearly of the same width (at the base) as the anterior teeth, they are much longer, the longest anterior tooth being only two-thirds as long as the shortest posterior tooth.

Seizing jaws (pl. 2, fig. 4), seven to ten, usually eight or nine. Curvature 41 to 51 per cent. Points with an oval base and imbedded from 20 to 25 per cent of their height into the shaft. Top of shaft and base of point converge in approaching edge of jaw. Edge of point nearly straight while the back is considerably curved. Pulp-canal displaced considerably toward

back of jaw, and extending into point from 60 to 70 per cent of its height. Pulp evenly distributed throughout canal.

Ovaries (pl. 2, fig. 1), long and slender. The mature ovary varies in length from 21.6 to 26.9 (in one case 32.3) per cent of total length of animal, and in width from 5.2 to 7.8 per cent of its length. It extends, when mature, beyond the posterior limit of anterior fin, although it never reaches the anterior limit of fin. Ovaries approaching maturity have not been noted in individuals under 22.1 mm. in length. Ova small even when mature.

S. californica is readily distinguished from all other species of *Sagitta* by its long collarette. In *S. planktonis* this structure extends caudally to the ventral ganglion, and in *S. ferox* to the anterior fins. In all other species its limit lies anterior to the ganglion. Thus the fact that the *collarette extends in S. californica from head to seminal vesicles* makes it utterly impossible to confuse it with any other known species.

Tabular Measurements.—As in my previous paper (1911) I have endeavored to include enough measurements in table 1 to enable a fairly accurate reconstruction of the outline of each individual considered, when taken in connection with the foregoing description. In addition, whenever the right ovary differed conspicuously in length from the left one, both were measured, and in the table the length of the left ovary appears below that of the right one. In anterior and posterior teeth and seizing jaws the number in both right and left rows is given, the latter following the former. Finally the following symbols are used to designate the stage of maturity in ovary and seminal vesicle:

inv.—invisible.
v. rem.—very remote from maturity.
rem.—remote from maturity.
imm.—immature.
w. dev.—well developed.
appr.—approaching maturity.
mat.—fully mature.

TABLE 1

Measurements of *Sagitta californica*[1]

Number	Length in mm.	Width	Tail		Length of ventral ganglion	Anterior fin			Posterior fin		
			Length	to ventral ganglion		Length	Width	to ventral ganglion	Length	Width	to anterior fin
1	9.68	4.55	30.9	71.8	8.18	17.3	2.27	1.82	21.8	2.73	10.00
2	13.55	4.55	27.9	71.5	7.14	17.5	1.95	1.95	24.0	4.22	11.70
3	14.46	4.94	26.6	69.2	5.70	20.5	2.28	0.76	24.0	3.42	7.60
4	15.30	4.60	28.1	70.0	6.90	20.1	2.30	1.15	23.6	3.45	8.05
5	15.65	4.67	27.5	69.6	6.18	19.1	1.97	1.68	23.0	3.66	10.10
6	16.50	3.75	28.0	69.0	6.40	19.2	2.13	1.60	26.1	3.46	6.94
7	16.68	5.01	27.4	69.4	6.34	20.3	3.16	1.06	26.4	5.27	6.85
8	17.75	4.20	27.2	69.8	5.94	19.3	2.48	1.98	24.3	4.45	8.40
9	18.10	4.85	28.2	69.6	5.83	19.0	1.94	1.21	26.7	4.36	7.28
10	18.21	4.83	27.5	69.6	6.27	19.3	2.17	1.45	23.7	3.86	9.18
11	18.40	4.78	29.2	73.2	6.70	20.1	2.87	1.44	25.8	4.80	8.60
12	19.00	4.26	24.6	71.3	5.55	18.5	2.08	1.85	19.4	3.70	6.48
13	19.00	4.17	27.8	70.0	6.48	20.4	2.54	0.93	24.0	4.40	8.34
14	19.85	4.65	26.5	68.4	6.20	21.4	2.65	1.33	23.9	3.98	6.20
15	20.06	4.38	26.3	69.0	6.24	20.2	2.85	1.75	25.0	4.16	7.45
16	20.78	4.66	28.0	69.0	5.94	19.9	2.96	1.27	24.2	3.81	7.20
17	20.85	4.83	27.7	69.6	5.88	19.7	2.94	1.26	25.6	4.41	7.55
18	20.92	5.04	29.0	70.6	5.46	20.2	2.94	1.26	24.3	3.78	7.55
19	21.20	4.98	27.0	69.3	5.40	19.9	2.49	1.25	26.1	4.98	6.65
20	21.20	5.40	27.8	70.0	5.80	18.3	2.08	2.49	21.8	3.53	9.54
21	21.20	4.56	27.4	71.0	5.38	21.2	3.11	1.24	25.3	4.98	7.46
22	21.25	5.36	28.1	69.9	5.36	19.8	3.10	1.24	25.6	4.95	7.43
23	21.30	4.55	29.4	71.5	4.96	16.5	1.65	2.48	22.3	3.31	11.20
24	21.35	5.35	25.5	69.0	5.76	20.6	2.47	1.65	26.4	4.74	7.82
25	21.45	4.91	28.7	70.9	5.74	19.7	3.07	1.23	23.3	4.10	9.43

[1] All measurements, unless otherwise noted in table, given in per cent of total length of animal.
[2] Per cent of posterior fin in front of tail septum.

TABLE I

MEASUREMENTS OF *Sagitta californica*[1]

Posterior fin		Ovary					Stage of maturity		Number of			
		Length		Width								
to seminal vesicle	tail septum[2]	in mm	in per cent	in mm.	in per cent	to posterior fin[3]	Ovary	Seminal vesicle	Anterior teeth	Posterior teeth	Seizing jaws	Number
?	54.0	.....	.....	.. .	.... .	. . ..	inv.	inv.	?–3	4–4	6–8	1
?	51.5	0.53	3.90	0.04	8.40	— 8.45	v. rem.	inv.	3–3	?–6	7 7	2
3.42	54.0	2.64	11.40	0.35	13.20	— 1.52	imm.	mat.	6 6	12–13	9 9	3
		3.17	13.70		11.00	+ 6.76						
4.60	52.0	0.79	5.20	0.08	10.00	— 7.47	v. rem.	v. rem.	4–3	6–7	7 7	4
?	51.0	0.70	4.50	0.04	5.70	— 7.30	v. rem.	v. rem.	3–4	7 7	6–7	5
2.40	51.0	0.97	5.86	0.04	4.10	— 7.46	v. rem.	v. rem.	3 4	7–8	8–7	6
2.64	52.0	1.14	6.85	0.08	6.90	— 6.85	v. rem.	v. rem.	4–4	8 9	7–7	7
2.97	53.0	1.14	6.44	0.09	7.70	— 6.44	v. rem.	v. rem.	4–4	9–9	8 9	8
2.92	53.0	1.23	6.80	0.09	7.15	— 7.30	v. rem.	v. rem.	4–4	8–8	7–8	9
3.38	51.0	1.23	6.76	0.13	10.70	— 5.30	v. rem.	v. rem.	3–3	7 6	8–7	10
2.87	52.0	1.32	7.18	0.09	6.66	— 6.21	v. rem.	v. rem.	?	?	?	11
2.32	61.0	1.05	5.55	0.09	8.35	— 6.00	v. rem.	v. rem.	4–4	8–9	8 8	12
2.78	52.0	1.41	7.40	0.09	6.25	— 5.10	v. rem.	v. rem.	4 4	8 8	8 8	13
3.10	54.0	1.67	8.40	0.09	5.30	— 4.42	v. rem.	v. rem.	4 4	10–?	7–8	14
2.63	52.5	1.41	7.02	0.13	9.40	— 6.24	v. rem.	rem.	5 5	10 10	8 8	15
2.96	53.0	1.94	9.32	0.13	6.82	— 3.39	v. rem.	imm.	?	?	7–7	16
2.94	52.5	2.02	9.66	0.18	8.70	— 3.78	v. rem.	imm.	4–5	10–10	9–9	17
3.78	52.0	2.29	10.90	0.18	7.70	— 1.68	rem.	imm.	4–4	8–?	8 7	18
2.49	56.0	1.93	9.13	0.13	6.80	— 5.40	v. rem.	rem.	5–5	10–11	8–9	19
3.32	53.0	1.93	9.14	0.18	9.10	— 2.80	v. rem.	rem.	4–4	10–10	7–8	20
2.90	54.0	2.02	9.55	0.18	8.70	— 4.15	v. rem.	imm.	6–6	11–11	8 8	21
2.48	52.0	2.28	10.70	0.18	7.70	— 2.48	rem.	imm.	5–5	11–11	7 7	22
3.72	54.0	1.76	8.30	0.13	7.50	— 3.72	v. rem.	rem.	4–3	?–8	7–7	23
2.88	51.5	2.81	13.20	0.22	7.80	— 4.10	rem.	imm.	4 3	10 9	8 9	24
3.28	51.0	2.55	11.90	0.22	8.62	± 0.00	rem.	imm.	5–5	7–7	8 8	25

[3] Given in per cent of length of ovary.

[4] The + indicates that the ovary extends beyond anterior limit of posterior fin, the — that it falls short of that point.

TABLE 1—*Continued*

Measurements of *Sagitta californica*[1]

Number	Length in mm.	Width	Tail			Anterior fin			Posterior fin		
			Length	to ventral ganglion	Length of ventral ganglion	Length	Width	to ventral ganglion	Length	Width	to anterior fin
26	21.75	5.26	27.5	69.5	5.66	21.8	2.84	1.62	23.0	4.45	6.48
27	21.80	5.24	29.0	69.6	6.05	19.0	2.82	2.02	23.8	4.43	8.85
28	22.00	4.80	27.2	69.2	4.80	20.4	2.20	2.40	24.8	4.40	6.00
29	22.00	5.60	27.6	68.8	6.00	19.2	3.20	1.20	23.6	4.80	8.80
30	22.00	5.20	28.0	68.8	5.60	19.6	3.00	1.20	25.6	4.80	7.60
31	22.05	5.38	27.1	69.0	5.57	19.1	2.79	1.59	23.5	4.18	8.25
32	22.05	5.37	27.5	70.5	4.78	21.1	2.59	1.59	24.3	4.18	7.57
33	22.09	5.17	27.1	69.0	6.04	19.5	2.59	1.59	23.1	4.41	9.75
34	22.18	5.15	28.2	72.5	5.15	20.2	1.98	1.98	24.6	4.36	9.51
35	22.20	6.55	27.8	69.8	4.37	20.2	3.18	1.59	25.8	4.37	7.15
36	22.25	5.14	28.0	70.0	5.14	19.8	2.76	1.58	24.9	4.55	7.50
37	22.25	5.52	28.8	69.5	5.14	19.0	2.96	1.58	24.5	4.75	7.50
38	22.35	5.50	27.6	70.0	5.50	19.7	3.15	1.57	24.4	3.74	8.16
39	22.35	5.12	28.0	70.0	5.91	19.3	2.36	1.18	23.6	3.94	9.45
40	22.35	5.32	27.5	69.4	5.90	20.1	3.35	1.57	25.6	4.33	5.90
41	22.38	5.12	26.8	70.0	6.70	19.7	2.76	1.97	24.8	3.15	7.86
42	22.50	4.50	27.7	69.1	5.46	19.1	2.73	1.95	23.4	4.50	7.81
43	22.52	5.85	28.5	70.0	5.47	20.3	2.93	1.56	24.2	5.08	7.04
44	22.60	5.83	28.0	69.6	5.83	19.8	2.72	1.56	24.5	4.28	7.40
45	22.60	4.47	27.2	69.6	5.45	20.6	2.14	1.56	24.9	3.50	7.00
46	22.60	5.45	27.6	69.6	5.84	20.6	2.53	1.17	25.3	4.47	7.00
47	22.78	5.41	27.0	68.6	5.40	18.2	2.32	1.93	23.6	3.48	9.26
48	22.83	5.00	27.6	70.0	5.38	18.8	2.69	1.54	24.6	3.46	9.22
49	22.85	6.15	28.5	70.7	5.77	19.6	3.07	1.54	25.0	4.61	7.70
50	22.95	5.75	29.1	70.5	5.36	18.8	2.49	1.92	24.9	3.83	7.65

[1] All measurements, unless otherwise noted in table, given in per cent of total length of animal.
[2] Per cent of posterior fin in front of tail septum.

TABLE 1—*Continued*

MEASUREMENTS OF *Sagitta californica*[1]

Posterior fin		Ovary					Stage of maturity		Number of			
		Length		Width								
to seminal vesicle	tail-septum[2]	in mm.	in per cent	in mm.	in per cent[3]	to posterior fin[4]	Ovary	Seminal vesicle	Anterior teeth	Posterior teeth	Seizing jaws	Number
3.24	53.0	2.02	9.30	0.13	6.53	— 2.83	v. rem.	imm.	5–6	10–11	8–8	26
2.82	51.0	2.72	12.50	0.18	6.45	+ 0.40	imm.	imm.	5–5	10–10	8–9	27
3.60	53.0	2.90	13.20	0.26	9.10	± 0.00	imm.	w. dev.	6–5	10–11	8–9	28
3.20	51.0	2.55	11.60	0.26	10.30	— 0.40	rem.	mat.	5–5	10–10	8–8	29
3.60	52.5	2.20	10.00	0.18	8.00	— 2.40	v. rem.	imm.	6–6	11–11	8–9	30
3.58	52.5	3.96	17.90	0.26	6.70	+ 5.60	imm.	mat.	3–4	10–10	8–7	31
2.39	52.5	2.55	11.60	0.18	6.90	— 1.20	rem.	w. dev.	6–6	12–?	8–8	32
3.72	52.0	2.02	10.70	0.18	8.70	— 3.26	rem.	imm.	5–5	9–9	7–8	33
2.78	52.0	3.96	17.80	0.35	8.90	+ 5.15	w. dev.	mat.	6–6	11–11	8–9	34
3.57	51.0	4.40	19.90	0.35	8.00	+ 6.75	appr.	mat.	6–6	11–11	9–9	35
2.77	52.0	2.11	9.48	0.22	10.40	— 3.56	rem.	w. dev.	5–6	10–11	9–9	36
3.16	51.5	4.48	20.20	0.40	8.82	+ 7.50	appr.	mat.	5–5	10–11	9–9	37
		4.05	18.20		10.80	+ 5.52						
3.15	52.0	2.38	10.60	0.35	14.80	— 1.97	imm.	mat.	5–6	12–12	8–7	38
2.76	52.0	2.64	11.80	0.31	11.70	— 0.39	rem.	w. dev.	5–5	10–10	9–8	39
2.36	55.0	4.40	19.70	0.35	8.00	+ 5.50	w. dev.	w. dev.	5–5	15–14	9–9	40
3.15	54.0	4.40	19.70	0.35	8.00	+ 6.30	w. dev.	imm.	7–7	16–15	9–9	41
3.52	53.0	2.99	13.30	0.22	7.35	+ 0.78	rem.	mat.	6–6	11–11	9–9	42
3.12	51.5	3.08	13.70	0.22	7.15	— 1.17	rem.	appr.	5–4	8–9	8–8	43
3.90	52.0	2.64	11.70	0.26	10.00	— 1.17	rem.	mat.	5–4	10–10	8–8	44
3.11	53.0	1.76	7.30	0.18	10.00	— 5.45	v. rem.	imm.	5–4	10–10	9–9	45
2.72	52.0	2.99	13.20	0.22	7.35	± 0.00	rem.	imm.	4–4	9–8	8–8	46
3.48	51.0	1.93	8.50	0.18	9.10	— 3.48	rem.	imm.	6–6	11–11	9–9	47
2.69	51.5	3.96	17.30	0.31	7.80	+ 4.61	imm.	mat.	4–4	10–10	8–8	48
3.46	54.0	3.08	13.50	0.26	8.56	± 0.00	rem.	w. dev.	5–5	11–10	9–9	49
3.45	52.0	4.75	20.70	0.35	7.40	+ 7.65	w. dev.	mat.	7–5	14–14	9–9	50

[3] Given in per cent of length of ovary.

[4] The + indicates that the ovary extends beyond anterior limit of posterior fin, the — that it falls short of that point.

TABLE 1—*Continued*

Measurements of *Sagitta californica*[1]

Number	Length in mm.	Width	Tail		Length of ventral ganglion	Anterior fin			Posterior fin		
			Length	to ventral ganglion		Length	Width	to ventral ganglion	Length	Width	to anterior fin
51	22.98	5.75	28.0	69.7	4.98	20.3	1.92	1.53	24.9	3.83	7.28
52	23.02	5.34	27.9	70.0	5.73	20.2	2.10	1.53	23.6	4.00	8.90
53	23.15	5.14	28.5	70.4	5.70	20.2	2.09	1.14	25.1	3.70	7.23
54	23.30	5.28	26.8	68.6	5.65	20.4	2.26	1.13	23.4	3.02	7.90
55	23.30	5.28	27.2	69.0	5.28	20.0	1.89	1.51	23.8	3.58	7.93
56	23.30	5.28	27.2	69.7	5.28	20.0	2.64	1.52	23.8	4.15	8.67
57	23.30	5.28	26.4	69.5	5.66	21.1	2.26	0.76	24.5	3.40	8.30
58	23.50	5.24	27.0	69.5	5.62	20.6	1.80	1.50	24.7	3.37	7.50
59	23.58	5.97	27.2	68.6	4.85	19.4	1.87	1.49	22.0	3.36	9.34
60	23.58	5.96	27.6	70.8	5.60	19.4	2.88	1.49	25.7	4.47	8.58
61	23.62	6.31	28.2	70.0	5.20	19.7	3.34	1.86	25.0	4.46	7.05
62	23.62	5.20	26.8	69.1	5.20	19.7	2.04	1.11	23.8	3.34	8.93
63	23.75	5.55	29.2	71.5	4.80	21.1	2.59	1.48	24.8	3.74	6.66
64	23.75	5.55	29.2	70.3	5.18	19.3	2.96	1.85	24.0	4.07	7.77
65	23.75	5.92	27.4	69.6	5.55	19.6	3.15	1.48	24.4	4.45	7.77
66	23.75	5.55	27.4	70.0	4.81	19.6	2.22	1.48	23.3	2.96	9.25
67	23.78	5.50	27.0	70.0	5.14	19.8	2.94	1.65	23.5	4.04	8.06
68	23.81	5.54	28.8	71.2	5.54	20.3	2.22	1.48	24.6	4.06	8.11
69	23.95	5.52	28.0	70.0	5.52	20.2	2.39	1.47	25.0	4.05	7.35
70	24.00	5.13	27.0	69.1	5.50	20.9	2.56	1.46	24.9	3.30	6.95
71	24.00	5.50	27.8	70.6	5.50	19.4	2.93	1.47	24.9	3.66	8.42
72	24.00	5.50	27.5	69.6	5.50	18.3	2.20	2.20	23.4	3.30	9.15
73	24.05	5.48	27.4	70.5	5.11	20.0	2.74	1.83	24.8	4.01	7.66
74	24.10	6.20	26.6	69.0	5.48	20.4	2.19	1.82	24.4	3.83	7.30
75	24.10	5.28	27.0	69.4	5.84	19.7	2.56	2.19	23.4	3.65	8.02

[1] All measurements, unless otherwise noted in table, given in per cent of total length of animal.
[2] Per cent of posterior fin in front of tail septum.

TABLE 1—*Continued*

MEASUREMENTS OF *Sagitta californica*[1]

Posterior fin		Ovary					Stage of maturity		Number of			
		Length		Width								
to seminal vesicle	tail septum[2]	in mm.	in per cent	in mm.	in per cent[3]	to posterior fin[4]	Ovary	Seminal vesicle	Anterior teeth	Posterior teeth	Setæ on jaws	Number
2.68	51.0	2.72	11.90	0.18	6.45	— 0.75	rem.	mat.	6–6	11–11	9–9	51
3.05	52.0	3.52	15.30	0.35	10.00	+ 3.06	imm.	w. dev.	5–?	10–11	8–8	52
		3.12	13.50		11.30	+ 1.34						
3.42	53.0	4.57	19.80	0.26	5.77	+ 6.46	imm.	appr.	6–6	10–9	9–8	53
4.53	58.0	2.55	10.90	0.35	13.80	— 1.13	appr.	mat.	6–6	12–12	9–9	54
		2.99	12.80		11.80	+ 1.51						
3.02	52.0	5.18	22.20	0.35	6.80	+ 9.80	appr.	mat.	6–6	15–16	8–8	55
3.40	52.5	3.78	16.20	0.35	9.30	+ 3.77	imm.	mat.	?–?	11–11	8–7	56
3.02	52.0	6.60	28.30	0.44	6.66	+15.50	mat.	appr.	5–5	9–9	8–8	57
3.74	53.0	3.16	13.50	0.22	6.95	+ 0.37	imm.	appr.	5–5	11–10	9–9	58
3.73	51.0	4.40	18.70	0.35	8.00	+ 7.45	w. dev.	mat.	6–6	12–12	8–9	59
		4.22	17.90		8.30	+ 6.71						
1.86	54.0	5.19	22.00	0.48	9.34	+ 8.20	w. dev.	mat.	6–7	12–12	8–8	60
2.60	52.0	7.65	32.30	0.40	5.20	+19.30	mat.	mat.	5–6	12–12	9–9	61
2.97	53.0	4.67	19.70	0.40	8.50	+ 7.06	appr.	mat.	6–6	12–11	8–9	62
		4.32	18.20		9.18	+ 5.58						
3.74	52.0	4.84	20.40	0.35	7.30	+ 7.40	w. dev.	mat.	6–6	13–13	9–9	63
3.70	51.0	4.40	18.50	0.40	9.00	+ 6.30	w. dev.	mat.	5–5	12–11	8–8	64
2.96	54.5	5.36	22.60	0.40	7.40	+ 9.25	appr.	mat.	7–7	14–14	8–9	65
3.70	52.5	4.66	19.60	0.35	7.55	+ 7.40	w. dev.	mat.	6–6	11–11	9–8	66
3.30	53.0	4.66	19.50	0.40	8.50	+ 6.98	w. dev.	mat.	6–6	13–13	8–8	67
3.32	54.5	5.72	24.00	0.44	7.19	+11.40	appr.	appr.	7–6	13–14	9–9	68
3.31	51.5	5.90	24.60	0.44	7.47	+11.30	appr.	mat.	5–6	?–14	7–8	69
3.30	51.5	3.40	14.30	0.44	12.80	+ 1.46	appr.	mat.	5–6	12–12	9–9	70
3.66	54.5	3.87	16.10	0.35	9.10	+ 2.57	imm.	appr.	5–5	13–13	9–8	71
3.66	53.0	4.67	19.40	0.35	7.55	+ 6.96	w. dev.	w. dev.	6–6	11–11	8–9	72
3.64	54.0	7.12	29.50	0.35	4.95	+16.00	appr.	mat.	6–6	13–12	8–8	73
		6.50	27.00		5.40	+13.50						
2.19	52.0	4.93	20.40	0.35	7.15	+ 7.65	w. dev.	w. dev.	6–?	14–14	8–8	74
		4.40	18.30		8.00	+ 5.47						
4.00	53.0	6.15	25.60	0.40	6.44	+13.10	appr.	mat.	5–5	11–12	9–8	75

[3] Given in per cent of length of ovary.

[4] The + indicates that the ovary extends beyond anterior limit of posterior fin, the — that it falls short of that point.

TABLE 1—*Concluded*

Measurements of *Sagitta californica*[1]

Number	Length in mm.	Width	Tail			Anterior fin			Posterior fin		
			Length	to ventral ganglion	Length of ventral ganglion	Length	Width	to ventral ganglion	Length	Width	to anterior fin
76	24.20	5.10	27.6	68.0	5.45	21.4	2.90	1.45	24.4	4.36	8.00
77	24.25	5.61	27.2	68.8	5.44	19.9	1.81	1.45	23.5	3.62	8.33
78	24.25	5.80	27.5	69.2	5.43	18.8	2.36	1.82	23.2	3.98	8.34
79	24.25	4.71	26.1	68.8	5.80	19.2	2.64	2.17	23.0	4.35	8.34
80	24.38	5.77	27.1	69.3	5.40	19.5	2.17	2.17	23.1	3.61	8.30
81	24.42	5.39	27.0	69.4	5.39	19.4	2.16	1.80	23.0	3.24	9.35
82	24.45	6.11	27.0	68.6	5.75	18.0	2.16	2.16	23.4	4.14	9.00
83	24.55	5.74	27.6	69.5	5.74	19.4	1.97	1.43	25.4	4.65	7.79
84	24.55	5.37	28.7	70.6	5.37	19.7	2.51	1.79	23.0	4.30	8.25
85	24.60	5.25	28.5	70.0	4.82	20.6	3.07	1.31	26.3	4.82	6.14
86	24.70	5.70	27.4	70.5	5.34	19.9	1.78	1.07	23.5	3.55	9.60
87	24.75	5.34	27.6	69.0	5.34	20.1	2.48	0.89	24.5	3.73	8.17
88	24.80	5.67	27.3	68.9	5.42	18.8	2.66	1.77	24.4	3.54	8.50
89	24.85	5.30	28.8	70.5	4.61	19.5	2.83	2.83	22.7	3.54	8.86
90	24.85	6.35	26.9	69.6	4.95	19.4	2.65	1.77	23.3	3.71	8.84
91	24.85	4.95	26.9	70.0	5.30	21.2	2.83	1.06	25.1	3.71	7.07
92	24.90	5.30	28.3	74.2	4.59	21.2	2.83	1.77	25.1	3.36	7.40
93	24.98	5.80	27.8	70.5	4.94	20.0	2.64	1.76	25.3	4.23	7.40
94	25.02	5.96	28.4	69.0	5.26	17.5	2.10	1.75	23.8	3.86	8.78
95	25.08	6.28	27.0	70.0	5.24	21.3	2.45	1.40	24.5	4.01	7.00
96	25.20	5.76	27.6	68.8	5.25	21.0	2.80	1.40	24.5	4.54	7.00
97	25.25	5.92	26.8	69.0	5.23	19.2	2.44	1.05	24.4	3.31	8.71
98	25.50	5.85	28.0	70.0	5.17	19.7	2.41	1.72	24.1	3.79	7.93
99	25.65	5.48	26.7	70.0	5.15	20.2	2.06	1.71	23.6	3.77	7.88
100	25.95	5.42	28.4	69.4	5.09	19.3	2.03	2.03	23.7	3.72	7.45

[1] All measurements, unless otherwise noted in table, given in per cent of total length of animal.
[2] Per cent of posterior fin in front of tail septum.

TABLE 1—*Concluded*

MEASUREMENTS OF *Sagitta californica*[1]

Posterior fin		Ovary					Stage of maturity		Number of			
		Length		Width								
to seminal vesicle	tail septum[2]	in mm.	in per cent	in mm.	in per cent[3]	to posterior fin[4]	Ovary	Seminal vesicle	Anterior teeth	Posterior teeth	Seizing jaws	Number
3.27	52.0	6.25	25.80	0.44	7.05	+12.70	appr.	mat.	6–5	12–13	8–8	76
		6.69	27.60		6.57	+14.60						
3.26	51.0	4.35	17.90	0.35	8.10	+ 6.00	imm.	mat.	4–5	11–11	8–8	77
3.98	55.0	4.32	17.70	0.35	8.16	+ 5.06	w. dev.	mat.	6–5	12–12	8–8	78
3.99	54.5	6.25	25.70	0.48	7.75	+12.70	mat.	mat.	5–5	13–12	8–9	79
3.61	53.0	4.40	18.00	0.44	10.00	+ 5.78	w. dev.	appr.	5–5	10–10	9–9	80
3.60	51.5	5.55	22.60	0.44	7.90	+10.80	appr.	mat.	6–6	12–12	8–8	81
3.60	54.0	5.90	24.10	0.40	6.71	+11.50	appr.	mat.	5–4	10–10	9–8	82
3.22	52.0	5.18	21.10	0.44	8.50	+ 7.78	w. dev.	imm.	6–6	15–14	8–9	83
		5.36	21.80		8.20	+ 8.10						
3.94	53.0	5.55	22.60	0.40	7.15	+10.40	appr.	mat.	7–7	13–14	8–9	84
2.19	52.0	1.76	8.77	0.13	7.50	— 4.82	v. rem.	imm.	5–5	10–10	7–8	85
3.20	51.5	5.10	20.60	0.44	8.60	+ 8.55	w. dev.	mat.	6–6	13–12	9–8	86
		5.55	22.40		7.95	+10.30						
3.02	51.0	6.03	24.30	0.44	7.30	+11.90	mat.	mat.	5–6	14–15	9–10	87
		6.20	25.00		7.10	+12.6						
2.83	51.0	4.93	19.80	0.40	8.04	+ 7.45	w. dev.	mat.	5–6	14–13	8–8	88
		4.23	17.00		9.58	+ 4.60						
4.25	51.5	4.40	17.70	0.35	8.00	+ 6.01	imm.	mat.	5–5	12–11	9–9	89
3.18	54.5	3.74	15.00	0.35	9.40	+ 2.30	imm.	mat.	5–6	14–14	8–8	90
2.83	55.0	4.93	19.80	0.40	8.03	+ 6.00	w. dev.	w. dev.	6–6	13–13	9–9	91
3.18	51.0	4.40	17.70	0.35	8.00	+ 4.76	appr.	mat.	6–6	11–12	10–9	92
2.72	53.0	5.81	22.20	0.44	7.60	+ 9.85	appr.	mat.	5–5	12–12	8–8	93
3.86	53.0	6.06	24.20	0.35	5.80	+11.90	mat.	mat.	6–6	12–12	9–9	94
		5.54	22.10		6.35	+10.50						
2.80	53.0	6.77	26.90	0.44	6.50	+13.30	mat.	mat.	6–6	13–14	9–9	95
		5.98	23.80		7.35	+10.50						
2.80	53.0	6.34	25.20	0.44	6.95	+12.20	mat.	mat.	7–7	15–12	9–9	96
		6.70	26.60		6.56	+13.60						
3.48	54.0	6.34	25.10	0.44	6.95	+11.80	appr.	mat.	6–7	14–15	8–8	97
3.79	53.0	5.18	20.30	0.40	7.60	+ 7.58	w. dev.	mat.	7–7	13–13	8–9	98
3.77	56.5	7.48	29.10	0.44	5.87	+15.80	mat.	mat.	6–5	13–12	9–9	99
		6.52	25.30		6.75	+12.00						
3.72	51.5	5.63	21.60	0.44	7.80	+ 9.50	mat.	mat.	5–6	14–15	9–10	100

[3] Given in per cent of length of ovary.

[4] The + indicates that the ovary extends beyond anterior limit of posterior fin, the — that it falls short of that point.

VARIATION AND CORRELATION IN PROPORTIONAL MEASUREMENTS

As the size of an organism at any particular developmental stage is merely the summation of the extents to which each region of its body has grown, it follows that the dimensions of any region are functions of the size attained by the organism. For this reason proportional instead of direct measurements are commonly used in taxonomy as of greater specific constancy. Still the reliability of such proportions depends upon whether the particular region measured grows at approximately the same rate as that of the entire animal or at a very different rate. Should the rates differ then the proportion would vary as the animal grows larger, and if the variation be considerable it might cause much confusion in identification and synonymy unless the direction and extent of such variation were known.

For instance, the tail in *S. californica* is defined as varying in length between 24 and 31 per cent of the length of animal. Suppose another similar species be discovered and defined as having a tail varying from 34 to 37 per cent in length, and as being smaller in size. The new species would be valid if the tail of its individuals were known to increase in length at approximately the same rate as the body, for the proportion (34 to 37) would then be constant, whatever the length of the animal. But, if the rate of increase in length of tail were *less* than the rate of increase in length of body, then the proportion—$\frac{\text{length of tail}}{\text{length of animal}}$—would be less in the larger animals and consequently the new species might be synonymous with *S. californica.* Accordingly if, to the definition of *S. californica,* we add that the variation of the length of tail between 24 and 31 per cent is *constant irrespective of the length of animal* or that it *varies directly or inversely as the animal grows larger,* such confusion could not arise.

Some space is therefore devoted to determining to what extent each of the proportional measurements given in table 1 is independent of, or dependent on, the length of animal.

Width of Body.—The body varies in width from 3.75 to somewhat over 6.25 per cent of the length. Separating the 100 specimens measured into six groups, each of which has a variation in width of 0.5 per cent, and then splitting each of these groups into seven sub-groups with reference to differences in length of animal, the following correlation table may be constructed which shows that the width-per cent is greatest in the larger animals.

TABLE 2

Correlation between Width-Per Cent and Length of Animal

Width per cent	Length of animal in mm.							
	12–14	14–16	16–18	18–20	20–22	22–24	24–26	Total
3.75–4.24	....	....	2 (67)	1 (14)	....	....	....	3
4.25–4.74	2 (100)	2 (67)	....	3 (43)	4 (22)	3 (7)	1 (4)	15
4.75–5.24	....	1 (33)	1 (33)	3 (43)	7 (39)	9 (21)	2 (7)	23
5.25–5.74	....	....	....	....	7 (39)	21 (49)	14 (50)	42
5.75–6.24	....	....	....	....	....	8 (18)	9 (32)	17
6.25–6.74	....	....	....	....	....	2 (5)	2 (7)	4
Total	2	3	3	7	18	43	28	104

$r = 0.6191 \pm 0.06047$

Examination of the numbers in brackets shows further that the width-per cent is least in the smaller animals, for in 43 per cent of those varying between 18 and 20 mm. in length the width-per cent is 4.25–4.75, while the same width-per cent occurs in only 22 per cent of those between 20 and 22 mm. in length, in 7 per cent of those between 22 and 24 mm., and in only 4 per cent of those between 24 and 26 mm. Furthermore, while the majority of animals whose lengths vary between 22 and 26 mm. have a width-per cent of 5.25–5.75, a larger proportion of those between 22 and 24 mm. have a smaller width-per cent and a larger proportion of those between 24 and 26 mm. have a greater width-per cent. It is therefore obvious that specimens of *S. californica* increase in width more rapidly than in length. Hence the following facts, extracted from table 4, are of specific importance:

1. The majority of specimens between 22 and 26 mm. in length have a width lying between 5.25 and 5.75 per cent.

2. The majority between 20 and 22 mm. have a width of 4.75–5.75 per cent.

3. The majority between 12 and 20 mm. have a width of 3.75–4.75 per cent.

4. The average width of specimens between 18 and 20 mm. is 4.65 per cent.

5. The average width of those between 20 and 22 mm. is 5.07 per cent.

6. The average width of those between 22 and 24 mm. is 5.24 per cent.

7. The average width of those between 24 and 26 mm. is 5.76 per cent.

8. For every increase of 1 mm. in length there is, *on the average*, an increase of 0.16 per cent in width.

Length of Ventral Ganglion.—Table 3 shows a pronounced negative correlation between length of animal and proportional length of ganglion, for only in those animals over 22 mm. in length is the ganglion less than 5.25 per cent, and only in those

TABLE 3

Correlation between Length of Animal and Proportional Length of Ventral Ganglion

Proportional length of ventral ganglion	Length of animal in mm.							
	12–14	14–16	16–18	18–20	20–22	22–24	24–26	Total
4.25–4.74	....	....	....	....	....	1 (2)	1 (4)	2
4.75–5.24	....	....	....	....	4 (22)	14 (33)	10 (36)	28
5.25–5.74	....	1 (33)	....	1 (14)	7 (39)	21 (49)	15 (53)	45
5.75–6.24	....	1 (33)	1 (33)	3 (43)	7 (39)	6 (14)	2 (7)	20
6.25–6.74	....	....	2 (67)	3 (43)	....	1 (2)	....	6
6.75–7.24	1 (50)	1 (33)	....	....	....	....	....	2
7.25–7.74	....	....	....	....	....	....	....	0
7.75–8.24	1 (50)	....	....	...	....	....	....	1
Total	2	3	3	7	18	43	28	104

$r = -0.62154 \pm 0.03059$

under 16 mm. in length is the ganglion greater than 6.75 per cent. This visual evidence is corroborated by the correlation coefficient, which is negative and more than twenty times the probable error. Moreover, examination of the numbers in brackets shows that, when the ganglion is less than 5.75 per cent, the proportion of the population having a ganglion of that length increases with the length of animal, while, when the ganglion is greater than 5.75 per cent, the proportion decreases as the animal increases in length. This becomes especially clear when arranged as follows:

14 per cent of animals 18–20 mm. have ganglion less than 5.75 per cent.
61 per cent of animals 20–22 mm. have ganglion less than 5.75 per cent.
84 per cent of animals 22–24 mm. have ganglion less than 5.75 per cent.
93 per cent of animals 24–26 mm. have ganglion less than 5.75 per cent.

86 per cent of animals 18–20 mm. have ganglion more than 5.75 per cent.
39 per cent of animals 20–22 mm. have ganglion more than 5.75 per cent.
16 per cent of animals 22–24 mm. have ganglion more than 5.75 per cent.
7 per cent of animals 24–26 mm. have ganglion more than 5.75 per cent.

Furthermore, when the average proportional length of ganglion corresponding to each of these groups is calculated, it becomes quite clear that the animal increases in length faster than the ganglion does. Here are the averages:

7.50 per cent for animals between 12 and 14 mm.
6.16 per cent for animals between 14 and 16 mm.
6.33 per cent for animals between 16 and 18 mm.
6.14 per cent for animals between 18 and 20 mm.
5.58 per cent for animals between 20 and 22 mm.
5.41 per cent for animals between 22 and 24 mm.
5.32 per cent for animals between 24 and 26 mm.

Now if, on account of their small number, we eliminate from consideration those animals under 18 mm. in length and examine these averages further, expressing the length of animals between 18 and 20, 20 and 22, 22 and 24, and 24 and 26 mm. in terms of their averages 19, 21, 23, and 25 mm., the following facts are revealed:

1. An increase in length from 19 to 21 mm. is accompanied on the average with a relative decrease in length of ganglion of 0.56 per cent.

2. An increase in length from 21 to 23 mm. is accompanied with a relative decrease in length of ganglion of 0.17 per cent.

3. An increase in length from 23 to 25 mm. is accompanied with a relative decrease in length of ganglion of 0.09 per cent.

These facts mean that the rates of increase in length of body and ganglion approximate closer to equality as the animal grows larger. In other words the ratio $\frac{\text{length of ganglion}}{\text{length of animal}}$ is more nearly constant in the larger than in the smaller animals.

Interval from Anterior to Posterior Fin.—Table 4 shows an absence of any well-defined correlation. Moreover it is

TABLE 4

Correlation between Length of Animal and Proportional Interval from Anterior to Posterior Fin

Proportional length of interval from anterior fin to posterior fin	Length of animal in mm.							
	12–14	14–16	16–18	18–20	20–22	22–24	24–26	Total
5	....	....	....	....	....	1 (2)	....	1
6	....	....	2 (67)	2 (29)	3 (17)	2 (5)	1 (4)	10
7	....	1 (33)	....	2 (29)	9 (50)	22 (51)	11 (39)	45
8	....	1 (33)	1 (33)	2 (29)	3 (17)	10 (23)	13 (46)	30
9	....	....	....	1 (14)	2 (11)	8 (19)	3 (11)	14
10	1 (50)	1 (33)	....	....	....	....	....	2
11	1 (50)	....	....	....	1 (5)	....	....	2
Total	2	3	3	7	18	43	28	104

$r = -0.1454 \pm 0.06468$

evident that, excepting the two specimens whose lengths lie between 12 and 14 mm., in the vast majority of all animals, irrespective of length, this interval measures between 7 and 9 per cent. However, the following averages indicate that there is at least a tendency for this interval to increase in length more rapidly than the animal does, and that the negative coefficient is probably due to the effect of those animals under 16 mm. in length in which the interval seems to be larger. These averages are as follows:

11.0 per cent in animals between 12 and 14 mm.
8.8 per cent in animals between 14 and 16 mm.
7.2 per cent in animals between 16 and 18 mm.
7.8 per cent in animals between 18 and 20 mm.
7.9 per cent in animals between 20 and 22 mm.
8.0 per cent in animals between 22 and 24 mm.
8.2 per cent in animals between 24 and 26 mm.

Interval from Posterior Fin to Seminal Vesicle.—In the 100 specimens measured in table 1, all stages in the maturity of seminal vesicle are recorded, from an invisible and barely visible condition in animals 12 to 14 mm. in length to complete maturity in the larger animals. In some species an interval exists between posterior fin and vesicle during the undeveloped stages of the vesicle which entirely disappears when the vesicles attain maturity. I was therefore led to expect that a negative correlation would be found in *S. californica* between the proportional length of this interval and length of animal. Imagine my surprise when table 5 was constructed and a tendency toward *positive* correlation revealed.

TABLE 5

Correlation between Length of Animal and Proportional Length of Interval between Posterior Fin and Seminal Vesicle

Proportional length of interval from posterior fin to seminal vesicle	Length of animal in mm.							
	12–14	14–16	16–18	18–20	20–22	22–24	24–26	Total
2.0–2.4	....	....	1 (33)	1 (14)	3 (17)	3 (7)	2 (7)	10
2.5–2.9	....	....	2 (67)	4 (57)	6 (33)	9 (21)	5 (18)	26
3.0–3.4	....	1 (50)	....	2 (29)	4 (22)	17 (40)	8 (29)	32
3.5–3.9	....	....	....	....	5 (28)	13 (30)	11 (39)	29
4.0–4.4	....	....	....	....	....	....	2 (7)	2
4.5–4.9	....	1 (50)	....	....	....	1 (2)	....	2
Total	0	2	3	7	18	43	28	101

$r = +0.165 \pm 0.0653$

Inspection of this table shows that, with two exceptions, the larger intervals are found only in the larger animals. Furthermore, inasmuch as the proportion of the population (see numbers

in brackets) possessing the interval measuring 2.5–2.9 per cent decreases as the length of animals increases, while the proportion possessing the larger interval measuring 3.5–3.9 per cent increases as the length of animals increases, it is evident that there is a pronounced tendency toward positive correlation in spite of the smallness of the coefficient ($r = +0.165$). Again, the fact that the majority of animals between 16 and 22 mm. have an interval measuring 2.5–2.9 per cent, while the majority of those between 22 and 24 mm. have an interval of 3.0–3.4 per cent, and the majority of those between 24 and 26 mm. have an interval of 3.5–3.9 per cent—points once more toward positive correlation. Finally, the following averages of interval measurements, excepting that for animals 14 to 16 mm., increase with considerable uniformity as the animals increase in length, pointing again toward positive correlation. Here are the averages:

4.00 per cent for animals between 14 and 16 mm.
2.58 per cent for animals between 16 and 18 mm.
2.82 per cent for animals between 18 and 20 mm.
3.05 per cent for animals between 20 and 22 mm.
3.26 per cent for animals between 22 and 24 mm.
3.36 per cent for animals between 24 and 26 mm.

Length of Ovary.—Excepting the articles by Ritter-Zahony (1908, 1910) and myself (1911), nothing has been published in which the ovary has been considered of specific importance. Its exclusion has been due to the fact that the ovary is the last structure to develop, so that one could find ovaries of any size in specimens otherwise fully mature. Nevertheless its average and maximum extent and correlations with the length of animal, as in table 6, reveal important characteristics for the species.

While this table, together with the coefficient ($r = +0.8998$), shows that the ovary increases in length much faster than the animal does, it also shows (1) that ovaries measuring less than 5 per cent were not found in animals over 16 mm. in length, and (2) that ovaries measuring more than 15 per cent were not found in animals under 22 mm. in length. Since we find (see table 1) that the ovary does not reach maturity until its length is over 20 per cent of that of the animal, these facts show that

TABLE 6

CORRELATION BETWEEN LENGTH OF ANIMAL AND PROPORTIONAL LENGTH OF OVARY

Proportional length of ovary	Length of animal in mm.							
	12–14	14–16	16–18	18–20	20–22	22–24	24–26	Total
0–4	4 (100)	2 (29)	....	....	....	....	....	6
5–9	....	3 (52)	5 (100)	12 (100)	14 (48)	5 (6)	2 (4)	41
10–14	....	2 (29)	....	....	15 (52)	27 (33)	2 (4)	46
15–19	....	....	....	....	....	32 (39)	18 (32)	50
20–24	....	....	....	....	....	15 (18)	19 (33)	34
25–29	....	....	....	....	....	1 (1)	16 (28)	17
30–34	....	....	....	....	....	2 (2)	....	2
Total	4	7	5	12	19	82	57	196

$r = +0.8998 \pm 0.0092$

the ovary in *S. californica* does not mature in individuals under 22 mm. in length. The table, however, tells us more than this. Mere cursory examination reveals the following facts:

1. In animals under 14 mm. the ovary is less than 5 per cent in length.

2. In animals 14 to 16 mm. the ovary is less than 15 per cent in length, and in the majority it varies between 5 and 10 per cent.

3. In the majority of animals 16 to 20 mm. the ovary varies from 5 to 10 per cent in length.

4. In the majority of those 20 to 22 mm. the ovary varies from 10 to 15 per cent in length.

5. In the majority of those 22 to 24 mm. the ovary varies from 15 to 20 per cent in length.

6. In the majority of those 24 to 26 mm. the ovary varies from 20 to 25 per cent in length.

Again, the average proportional length of ovary, corresponding to each group of animals differing by 2 mm. in length, as calculated from table 6 and as obtained directly from table 1, is as follows:

Length of animal in mm.	Calculated average	Actual average
12–14	2.5 per cent	3.9 per cent
14–16	7.5 per cent	8.7 per cent
16–18	7.5 per cent	6.2 per cent
18–20	7.5 per cent	7.0 per cent
20–22	10.1 per cent	10.8 per cent
22–24	16.7 per cent	17.0 per cent
24–26	21.5 per cent	21.7 per cent

Comparison of the calculated and actual averages reveals little difference, especially in the larger and more numerous animals. It is quite safe, therefore, to conclude that, if based on a fairly large number of measurements, the average length of ovary in *S. californica* will vary with the length of animals measured, as follows:

0–5 per cent in animals between 0 and 14 mm.
5–10 per cent in animals between 14 and 20 mm.
8–15 per cent in animals between 20 and 22 mm.
15–19 per cent in animals between 22 and 24 mm.
19–25 per cent in animals between 24 and 26 mm.

Length of Tail.—Preparing a correlation table, as given below, between length of tail as measured in per cent and length of animal, we see that there is very little if any definite relation between the larger animals and proportional length of tail.

TABLE 7

Correlation between Length of Animal and Proportional Length of Tail

Proportional length of tail	Length of animal in mm. 12–14	14–16	16–18	18–20	20–22	22–24	24–26	Total
24	....	....	....	1 (14)	....	....	....	1
25	....	....	....	....	1 (6)	....	....	1
26	....	1 (33)	....	2 (29)	1 (6)	4 (9)	5 (18)	13
27	1 (50)	1 (33)	2 (67)	2 (29)	9 (50)	24 (56)	16 (57)	55
28	....	1 (33)	1 (33)	1 (14)	4 (22)	12 (28)	7 (25)	26
29	....	....	....	1 (14)	3 (16)	3 (7)	....	7
30	1 (50)	....	....	....	....	....	....	1
Total	2	3	3	7	18	43	28	104

$r = -0.0858 \pm 0.06565$

While the correlation coefficient is negative ($r = -0.0858$), thereby indicating that the body increases in length faster than the tail, the probable error is relatively so large ($= 0.0656$) that this appearance is most likely due to chance. It is evident from inspection of the table that the majority of animals between the lengths of 20 and 26 mm. have tails lying between 27 and 28 per cent. Furthermore the next most abundant number have tails lying between 28 and 29 per cent. Moreover, when the average lengths for the tail corresponding to each group of animals are calculated they show more clearly the absence of any definite correlation. Such averages are as follows:

27.9 per cent for entire population (12–26 mm).
27.6 per cent for animals between 24 and 26 mm.
27.1 per cent for animals between 22 and 24 mm.
27.9 per cent for animals between 20 and 22 mm.
27.2 per cent for animals between 18 and 20 mm.
27.8 per cent for animals between 14 and 16 mm.
27.5 per cent for animals between 14 and 16 mm.
29.0 per cent for animals between 12 and 14 mm.

Thus, excepting those animals between 12 and 14 mm., the average length of tail lies between 27 and 28 per cent, irrespective of the length of animal. It is quite probable, therefore, that, between the lengths of 14 and 26 mm., the tail grows as fast and no faster than the body, thereby maintaining a constant proportion.

Remaining Proportions.—As in the case of the tail, no definite correlation between variations in length of animal and variations in the remaining proportions was found. It seems unnecessary, therefore, to consider each in detail. Instead the correlation coefficients relative to each proportion, given below, show clearly the absence of definite correlations:

Proportions	Coefficients
Interval from tail to ventral ganglion	$r = -0.1403 \pm 0.053$
Length of anterior fin	$r = +0.154 \pm 0.096$
Width of anterior fin	$r = +0.0931 \pm 0.0656$
Anterior fin to ventral ganglion	$r = +0.1485 \pm 0.0647$
Length of posterior fin	$r = +0.0353 \pm 0.0661$
Width of posterior fin	$r = +0.0679 \pm 0.066$

To corroborate the evidence of the coefficients the average measurements of each proportion corresponding to each length of animal are here appended:

Interval from Tail to Ventral Ganglion

69.8 per cent for animals between 24 and 26 mm.
70.0 per cent for animals between 22 and 24 mm.
69.8 per cent for animals between 20 and 22 mm.
70.4 per cent for animals between 18 and 20 mm.
69.5 per cent for animals between 16 and 18 mm.
69.8 per cent for animals between 14 and 16 mm.
71.5 per cent for animals between 12 and 14 mm.

Length of Anterior Fin

19.9 per cent for animals betwen 24 and 26 mm.
19.9 per cent for animals between 22 and 24 mm.
19.8 per cent for animals between 20 and 22 mm.
20.0 per cent for animals between 18 and 20 mm.
19.8 per cent for animals between 16 and 18 mm.
20.2 per cent for animals between 14 and 16 mm.
17.5 per cent for animals between 12 and 14 mm.

Width of Anterior Fin

2.43 per cent for animals between 24 and 26 mm.
2.55 per cent for animals between 22 and 24 mm.
2.17 per cent for animals between 20 and 22 mm.
2.45 per cent for animals between 18 and 20 mm.
2.54 per cent for animals between 16 and 18 mm.
2.21 per cent for animals between 14 and 16 mm.
2.12 per cent for animals between 12 and 14 mm.

Interval from Anterior Fin to Ventral Ganglion

1.32 per cent for animals between 24 and 26 mm.
1.59 per cent for animals between 22 and 24 mm.
1.61 per cent for animals between 20 and 22 mm.
1.39 per cent for animals between 18 and 20 mm.
1.58 per cent for animals between 16 and 18 mm.
1.25 per cent for animals between 14 and 16 mm.
1.75 per cent for animals between 12 and 14 mm.

Length of Posterior Fin

24.2 per cent fo ranimals between 24 and 26 mm.
24.3 per cent for animals between 22 and 24 mm.
24.4 per cent for animals between 20 and 22 mm.
25.5 per cent for animals between 18 and 20 mm.
25.8 per cent for animals between 16 and 18 mm.
24.2 per cent for animals between 14 and 16 mm.
23.0 per cent for animals between 12 and 14 mm.

Width of Posterior Fin

3.92 per cent for animals between 24 and 26 mm.
3.94 per cent for animals between 22 and 24 mm.
4.28 per cent for animals between 20 and 22 mm.
4.11 per cent for animals between 18 and 20 mm.
4.25 per cent for animals between 16 and 18 mm.
3.42 per cent for animals between 14 and 16 mm.
3.50 per cent for animals between 12 and 14 mm.

In the case of the length of the posterior fin there is an indication of a possible negative correlation, the proportion diminishing at the rate of about 0.05 per cent for an increase of 1 mm. in length of animal. However, as the average proportion, irrespective of the length, lies between 24.2 and 25.8 per cent, it is safe to conclude that the fin increases in length at approximately the same rate that the animal does.

VARIATION AND CORRELATION IN NUMBER OF TEETH AND SEIZING JAWS

The number of anterior and posterior teeth and seizing jaws is regarded by most investigators as of maximum significance in defining species of *Sagitta*. While I have suggested elsewhere (1911, p. 68), that "variations in number of both anterior and posterior teeth in many species is not referable to specific differences, but probably to some distribution factor," it is nevertheless true that certain facts concerning their manner and rate of variation are of considerable specific importance, as will be seen in the following remarks.

Number of Anterior Teeth.—Variation in number of anterior teeth is well revealed in the following histogram (text fig. 1), which shows that out of 191 tooth-rows counted in individuals varying from 9.5 to 26 mm. in length none had less than 3 nor more than 7 teeth, while about 6 per cent had 3, 17 per cent 4, 32.5 per cent 5, 37 per cent 6, and 8 per cent 7. Now, while these frequencies, together with the rate of increase till the maximum is attained, the rate of decrease thereafter, the position of the maximum, and other features of the histogram are definitely characteristic of the population considered, their

value as specific constants is impaired, owing to the effect of variation in length of individual upon the number of teeth possessed. In other words, if the number of teeth increase or decrease as the animal increases in length, it is evident that the

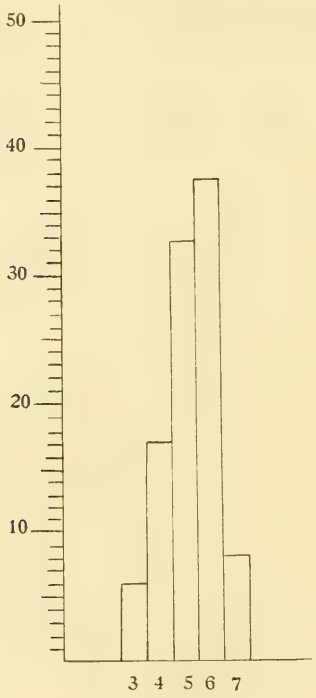


Fig. 1

nature of the histogram will vary according to the number of specimens of any particular length constituting the population considered. It is necessary, therefore, to ascertain the relation between number of teeth and length of specimen.

TABLE 8

CORRELATION BETWEEN NUMBER OF ANTERIOR TEETH AND LENGTH OF ANIMAL

Number of teeth	Length of animal in mm.							Total
	12–14	14–16	16–18	18–20	20–22	22–24	24–26	
3	3	2	1	2	3	1	....	12
	(100)	(33)	(17)	(17)	(9)	(1)		
4	....	2	5	8	8	8	2	33
		(33)	(83)	(66)	(24)	(10)	(4)	
5	....	....	....	2	15	27	20	64
				(17)	(44)	(32)	(36)	
6	....	2	....	....	8	40	25	75
		(33)			(24)	(48)	(46)	
7	....	....	....	....	....	7	8	15
						(8)	(15)	
Total	3	6	6	12	34	83	55	199

$$r = +0.609 \pm 0.0300$$

Table 8 shows that the greater number of teeth is possessed only by the larger animals. Furthermore, when the upper "row" of the table is expressed in percentages of the total population of each "column" (see numbers in brackets), it is evident that the smaller number of teeth is associated with the shorter animals. Moreover, when all these percentages are examined the following facts relative to the number of teeth possessed by the majority of animals are apparent:

Majority between	have
12 and 14 mm.	3 teeth
14 and 20 mm.	4 teeth
20 and 22 mm.	5 teeth
22 and 26 mm.	6 teeth

These facts show that the histogram (text fig. 1) is approximately true only for animals over, but not under, 22 mm. in length.

NUMBER OF POSTERIOR TEETH.—The number of posterior teeth varies from 4 to 16 in animals varying from 9.5 to 26 mm. in length. The accompanying histogram shows that no indi-

vidual had 3, 5 or more than 16 teeth, while, out of 189 tooth-rows counted, about 1 per cent had 4, 2 per cent 6, 4 per cent 7, 5.5 per cent 8, 6.5 per cent 9, 19.5 per cent 10, 19.5 per cent 11, 17.5 per cent 12, 11 per cent 13, 9 per cent 14, 4 per cent 15, and less than 1 per cent 16.

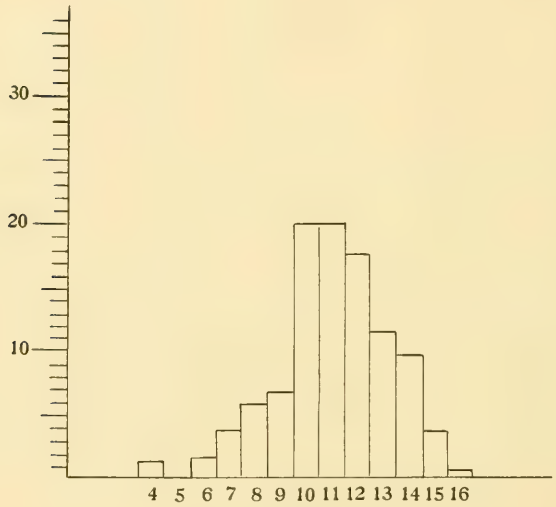


Fig. 2

Here again the specific validity of this histogram depends upon to what extent the number of teeth is correlated with length of animal. Concerning this table 9 shows an even greater correlation than that displayed by the anterior teeth. This visual impression is corroborated by the coefficients, that relating to the anterior teeth being 0.609 ± 0.0300 and that relating to the posterior teeth 0.751 ± 0.021. Here it is perfectly evident that the smaller animals have the fewest and the larger animals

TABLE 9

CORRELATION BETWEEN LENGTH OF ANIMAL AND NUMBER OF POSTERIOR TEETH

Number of teeth	Length of animal in mm.							Total
	12–14	14–16	16–18	18–20	20–22	22–24	24–26	
4–5	2 (67)	....	....	....	....	....	....	2
6–7	1 (33)	4 (67)	1 (17)	2 (18)	2 (7)	....	....	10
8–9	....	....	5 (83)	8 (73)	5 (16)	9 (11)	....	27
10–11	....	....	....	1 (9)	23 (74)	39 (48)	10 (18)	73
12–13	....	2 (33)	....	....	1 (3)	22 (26)	31 (55)	56
14–15	....	....	....	....	....	10 (12)	15 (27)	25
16–17	....	....	....	....	....	2 (3)	....	2
Total	3	6	6	11	31	82	56	195

$r = 0.7506 \pm 0.02109$

the most teeth. Moreover when we consider the numbers in brackets the following facts are revealed:

Majority of animals between	have
12 and 14 mm.	4–5 teeth
14 and 16 mm.	6–7 teeth
16 and 20 mm.	8–9 teeth
20 and 24 mm.	10–11 teeth
24 and 26 mm.	12–13 teeth

These facts make it obvious that the histogram (text fig. 2) is approximately true only for animals between 20 and 24 mm. in length, and even here the approximation is slight, for the rate of addition of teeth with an increasing length of animal is rapid. This histogram, then, can only be regarded as specifically constant when the population considered consists of a similar proportion of individuals of the various lengths to that upon which it is based.

Number of Seizing Jaws.—These structures we found to vary from 6 to 10, the usual number being 8 or 9. Text figure 3 shows

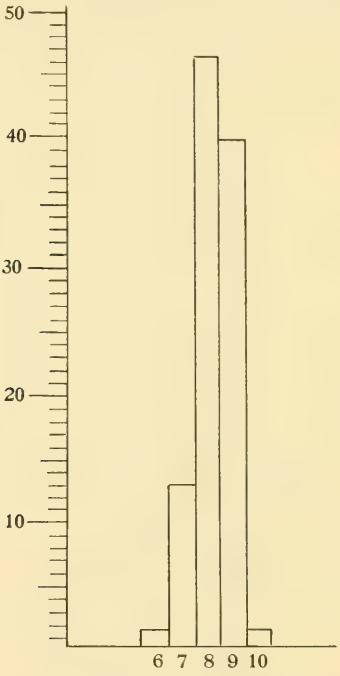


Fig. 3

in addition that out of 198 rows of jaws about 1 per cent had 6 jaws, while 13 per cent had 7, 46 per cent 8, 39 per cent 9, and 1 per cent 10.

However table 10, as well as its correlation coefficient ($r = 0.457 \pm 0.0372$) shows that, while the length of animal and number of jaws are positively associated, the correlation is not so pronounced as in the case of anterior and posterior teeth. Still an examination of the numbers in brackets reveals the following facts:

Majority of animals between	have
12 and 18 mm.	7 jaws
18 and 22 mm.	8 jaws
22 and 26 mm.	8–9 jaws

TABLE 10

CORRELATION BETWEEN LENGTH OF ANIMAL AND NUMBER OF SEIZING JAWS

Number of jaws	Length of animal in mm.							Total
	12–14	14–16	16–18	18–20	20–22	22–24	24–26	
6	1 (25)	1 (17)	....	....	....	....	....	2
7	2 (50)	3 (59)	3 (59)	3 (25)	9 (25)	5 (6)	1 (2)	26
8	1 (25)	....	2 (33)	9 (75)	20 (56)	38 (44)	28 (50)	98
9	....	2 (33)	1 (17)	....	7 (19)	43 (50)	25 (45)	78
10	....	....	....	....	....	....	2 (3)	2
Total	4	6	6	12	36	86	56	206

$r = 0.4566 \pm 0.0372$

SUMMARY

We have discovered in this discussion of variation and correlation many facts of specific importance as follows:

1. In animals between 12 and 26 mm. in length, variation in the ratio between length of animal and length of tail, interval from tail to ventral ganglion, length and width of anterior fin, interval from anterior fin to ventral ganglion, and length and width of posterior fin—is approximately constant, irrespective of the length of animal. Of all proportional measurements these are, therefore, the safest for the identification of *S. californica*, and this is especially true of the proportional length of tail.

2. In animals between 12 and 26 mm. the width of body, interval between anterior and posterior fins, interval from posterior fin to seminal vesicle, and length of ovary increase *more* rapidly than the animal increases in size, while the ventral ganglion increases *less* rapidly than the animal does. Therefore, the ratio between these various measurements and length of animal is of certain specific value only for animals of definite lengths.

TABLE 11

SUMMARY OF CHARACTERISTICS RELATIVE TO MAJORITY OF ANIMALS IN EACH LENGTH-GROUP*

A. Characteristics constant irrespective of length of animal

Length of animals in mm.	12–17	14–16	16–18	18–20	20–22	22–24	24–26
Length of tail	26–28	26–28	26–28	26–28	27–29	27–29	27–29
Tail to ventral ganglion	70–72	69–71	69–71	69–71	69–71	69–71	69–71
Length of anterior fin	?	19–21	19–21	19–21	19–21	19–21	19–21
Width of anterior fin	1.7–3.0	1.7–3.0	1.7–3.0	1.7–3.0	1.7–3.0	1.7–3.0	1.7–3.0
Anterior fin to ventral ganglion	1–2	1–2	1–2	1–2	1–2	1–2	1–2
Anterior to posterior fin	?	?	6–9	6–9	7–9	7–9	7–9
Length of posterior fin	?	23–26	23–26	23–26	23–26	23–26	23–26
Width of posterior fin	?	3–5	3–5	3–5	3–5	3–5	3–5

B. Characteristics dependent on length of animal

Number of anterior teeth	3	4	4	4	5	6	6
Number of posterior teeth	4–5	6–7	8–9	8–9	10–11	10–11	12–13
Number of seizing jaws	7	7	7	8	8	8–9	8–9
Width of body	3.7–4.8	3.7–4.8	3.7–4.8	4.2–5.3	4.7–5.8	4.7–5.8	5.2–6.3
Length of ventral ganglion	6.7–8.3	5.7–7.3	5.7–6.8	5.7–6.8	5.2–6.3	4.7–5.8	4.7–5.8
Posterior fin to vesicle	?	?	2–3	2.5–3.5	2.5–3.5	3–4	3–4
Length of ovary	0–5	5–10	5–10	5–10	10–15	10–20	15–25

* All measurements in per cent of total length of animal.

TABLE 12

SUMMARY OF CHARACTERISTICS RELATIVE TO THE AVERAGE PROPORTIONS IN ANIMALS OF EACH LENGTH-GROUP*

	12–14	14–16	16–18	18–20	20–22	22–24	24–26
A. Characteristics constant irrespective of length of animal							
Length of animals in mm.							
Length of tail	29.0	27.5	27.8	27.2	27.9	27.1	27.6
Tail to ventral ganglion	71.5	69.8	69.5	70.4	69.8	70.0	69.8
Length of anterior fin	17.5	20.2	19.8	20.0	19.8	19.9	19.9
Width of anterior fin	2.12	2.21	2.54	2.45	2.17	2.55	2.43
Anterior fin to ventral ganglion	1.75	1.25	1.58	1.39	1.61	1.59	1.32
Length of posterior fin	23.0	24.2	25.8	25.5	24.4	24.3	24.2
Width of posterior fin	3.50	3.42	4.25	4.11	4.28	3.94	3.92
B. Characteristics dependent on length of animal							
Length of ventral ganglion	7.50	6.16	6.33	6.14	5.58	5.41	5.32
Anterior to posterior fin	11.00	8.8	7.2	7.8	7.9	8.0	8.2
Posterior fin to vesicle	?	4.00	2.58	2.82	3.05	3.26	3.36
Length of ovary	2.5	7.5	7.5	7.5	10.1	16.7	21.5
Width of body	?	?	4.33	4.65	5.07	5.24	5.76

* Proportions given in per cent of total length of animal.

3. The number of anterior and posterior teeth and seizing jaws increases as the animal grows larger, the rate of increase being greatest in posterior teeth and smallest in seizing jaws. Therefore, the specific value in number of these structures depends not only on the extremes of variation but, quite as definitely, on the amount of variation in the *rates* of increase.

4. The maximum number of animals whose lengths vary within 1 mm. from 13, 15, 17, 19, 21, 23 and 25 mm. have the characteristics summed up in table 11.

5. The average proportions of the various regions of the body relative to animals varying between 12 and 14, 14 and 16, 16 and 18, 18 and 20, 20 and 22, 22 and 24, and 24 and 26 mm., are summed up in table 12.

It is needless to say that, in tables 11 and 12, the figures are not very reliable in the case of animals under 18 mm. in length because of the small number considered. For the others, however, the figures ought to hold good within a small range of variation if determined on the basis of a moderately large number of specimens. Furthermore, if *S. californica* should be discovered elsewhere than in California waters, these tables will furnish means for ascertaining the direction and degree of variation due to differences in locality.

DISTRIBUTION

Altogether 236 specimens were obtained, of which one was taken in a Nansen closing net haul (no. 2858) made from 150 to 100 fathoms, two in a similar haul (no. 2840) made from 10 to 5 fathoms, and the remainder from the surface. None were obtained prior to October 24, 1911, nor, so far as the hauls have been examined, since October 28, 1911. Furthermore, of the twenty-one surface hauls made, all but two obtained the species. Now the same localities from which this species was obtained were thoroughly investigated between the surface and 75 fathoms during every month of 1911, except September, and it seems probable that *S. californica* was not present prior to August 11th nor after November 27th, the former being the last date of hauling previous to October 24th, and the latter being the first

date of hauling after October 28th. The exact data concerning the October surface hauls are given in the accompanying table.

TABLE 13

DATA CONCERNING THE SURFACE CATCHES OF *Sagitta californica*.*

Haul number	Net	Date	Time	Station	Temperature, C.	Number of specimens
2785	000	Oct. 24	8:00– 8:45 a.m.	B	19.15	7
2800	000	Oct. 24	10:20–10:55 a.m.	B	19.3	11
2803	000	Oct. 24	11:10–12:30 a.m.	B	19.3	42
2821	000	Oct. 24	2:10– 3:07 p.m.	B	19.4	77
2826	000	Oct. 25	7:10– 8:10 a.m.	A	19.2	3
2829	000	Oct. 25	8:32– 9:40 a.m.	A	19.5	7
2842	000	Oct. 25	9:50–10:50 a.m.	A	20.1	1
2855	000	Oct. 25	11:00–12:00 a.m.	A	20.2	2
2861	000	Oct. 25	12:10–12:45 p.m.	A	?	19
2864	000	Oct. 25	1:00– 1:45 p.m.	A	19.9	6
2871	000	Oct. 26	7:50– 8:50 a.m.	A	19.2	5
2877	000	Oct. 26	9:00–10:20 a.m.	A	19.1	9
2883	000	Oct. 26	12:00–12:30 p.m.	A	19.4	1
2894	000	Oct. 27	7:00– 7:40 a.m.	B	18.6	18
2906	000	Oct. 27	12:00–12:30 p.m.	B	19.2	14
2909	000	Oct. 27	1:05– 1:55 p.m.	B	?	2
2917	000	Oct. 28	9:25– 9:45 a.m.	A	18.8	4
2921	000	Oct. 28	9:50–10:10 a.m.	A	?	4
2924	000	Oct. 28	10:20–10:45 a.m.	A	?	1

* *Station A* is located at 32° 22′.7 N, 117° 19′.2 W on a line extending WSW of South Coronado Island at a point approximately three and one-half miles from the island, where the water is 350 fathoms in depth.

Station B is located at 32° 22′.4 N, 117° 21′.2 W on the same line approximately two miles farther seaward, where the water is 700 fathoms in depth.

Owing to the small number of specimens obtained and owing to the fact that their capture was limited to four days of October, 1911, very little regarding their manner of distribution is determinable. However, table 13 reveals one interesting fact, namely, that the species was more abundant at station B than at station A, i.e., at the location farthest from land. Altogether 171 specimens were obtained from station B and 62 from station A, or an average of 22 per hour at B and 7 per hour at A. Furthermore this relation holds when the corresponding times of day are compared, as in table 14.

TABLE 14

Showing Relative Abundance of Species at A and B

Time of day	Station A				Station B			
			Specimens				Specimens	
	Hauls	Hours	Total	Per hour	Hauls	Hours	Total	Per hour
7 to 10 am	5	4.8	28	6	3	2.5	25	10
10 to 12:30 a.m.	5	3.2	9	3	4	3.6	67	19
12:30 to 3 p.m.	2	1.3	25	19	2	1.9	79	42

Should the reader exhaustively analyze table 13 with respect to this difference between the two locations he would realize that this appearance is probably not due to chance but to a definite correlation. It is, however, another matter to discover its significance. If this appearance be due to the distance from land then it would be legitimate to conclude that *S. californica* is mainly an oceanic species. On the other hand, *S. enflata* accompanied *S. californica* in nearly every haul and, as pointed out elsewhere (1911, p. 156), this may mean the occurrence of a tropical current, in which event we should expect the species to occur more abundantly nearer the current and therefore possibly farther from the coast. Had the investigations been extended over ten or fifteen stations at increasing distances from land some clue to the significance of this correlation would doubtless have been discovered, but as the matter now stands it seems unjustifiable to do more than point out these two possibilities.

Scripps Institution for Biological Research of the University of California, La Jolla, California.

Transmitted September 1, 1912.

LITERATURE CITED

MICHAEL, E. L.
1911. Classification and vertical distribution of the Chaetognatha of the San Diego region, including redescriptions of some doubtful species of the group. Univ. Calif. Publ. Zool., 8, 21–186, pls. 1–8.

PEARL, R.
1911. Biometric ideas and methods in biology, their significance and limitations. Scientia, 10, 101–119.

VON RITTER-ZÁHONY, R.
1908. Chätognathen. Ber. Comm. Enforsch. östl. Mittelmeer, Zool. Ergeben, 14, 18 pp. 1 Taf.
1910. Die Chätognathen. Fauna Arctica, 5, 251–288, Taf. 5.
1911. Revision der Chätognathen. Deutsche Südpolar Exped. 1901–1903, Bd. 13, Zool. 5, 71 pp., figg. im text.

EXPLANATION OF PLATE 2

All figures drawn with the camera lucida.

Fig. 1. Ventral view of *Sagitta californica*. × 10.

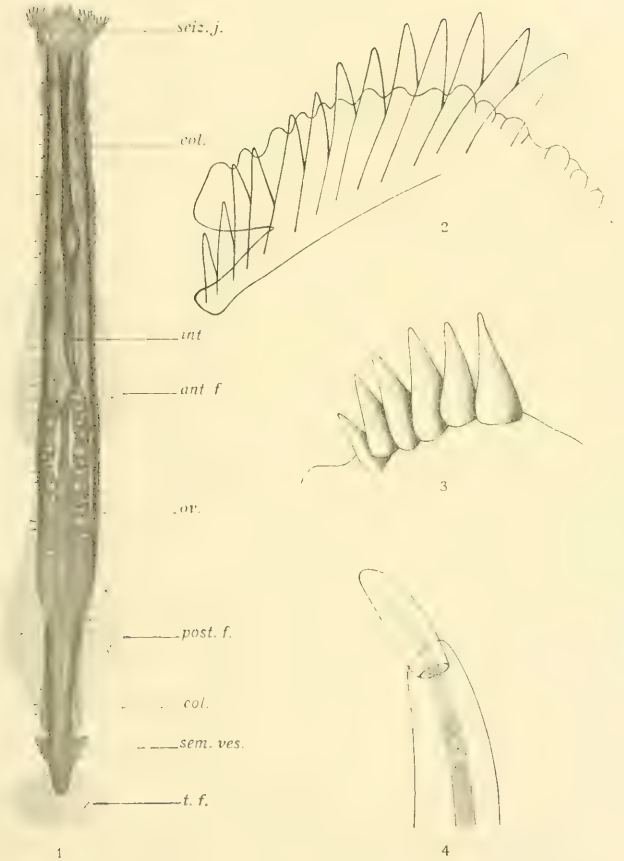
Fig. 2. Vestibular ridge of *Sagitta californica*. × 335.

Fig. 3. Anterior teeth of *Sagitta californica*. × 440.

Fig. 4. Seizing jaw of *Sagitta Californica*. × 1300.

ABBREVIATIONS

ant. f.—anterior fin.
col.—collarette.
int.—intestine.
ov.—ovary.
post. f.—posterior fin.
seiz. j.—seizing jaws.
sem. ves.—seminal vesicle.
t. f.—tail fin.



E.L.M., del. ad nat. Lith. Gottschalk, S.F.

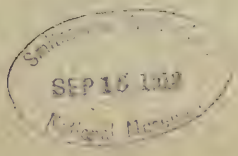
UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY
Vol. 11, No. 6, pp. 127-142, pls. 3-4 August 30, 1913

PYCNOGONIDA FROM THE COAST OF CALIFORNIA

WITH DESCRIPTIONS OF TWO NEW SPECIES

BY
HARRY V. M. HALL

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY



UNIVERSITY OF CALIFORNIA PUBLICATIONS

Note.—The University of California Publications are offered in exchange for the publications of learned societies and institutions, universities and libraries. Complete lists of all the publications of the University will be sent upon request. For sample copies, lists of publications or other information, address the Manager of the University Press, Berkeley, California, U. S. A. All matter sent in exchange should be addressed to The Exchange Department, University Library, Berkeley, California, U. S. A.

OTTO HARRASSOWITZ, LEIPZIG.

Agent for the series in American Archaeology and Ethnology, Classical Philology, Education, Modern Philology, Philosophy, Psychology, History.

R. FRIEDLAENDER & SOHN, BERLIN.

Agent for the series in American Archaeology and Ethnology, Botany, Geology, Geography, Mathematics, Pathology, Physiology, Zoology, and Memoirs.

ZOOLOGY.—W. E. Ritter and C. A. Kofoid, Editors. Price per volume, $3.50. Commencing with Volume II, this series contains Contributions from the Laboratory of the Marine Biological Association of San Diego.

Cited as Univ. Calif. Publ. Zool.

Volume 1, 1902-1905, 317 pages, with 28 plates $3.50

Volume 2 (Contributions from the Laboratory of the Marine Biological Association of San Diego), 1904-1906, xvii + 382 pages, with 19 plates $3.50

Volume 3, 1906-1907, 383 pages, with 23 plates $3.50

Volume 4, 1907-1908, 400 pages, with 24 plates $3.50

Volume 5, 1908-1910, 440 pages, with 34 plates $3.50

Vol. 6.

1. (XXIII) On the Weight of Developing Eggs. Part I, The Possible Significance of Such Investigations, by William E. Ritter; Part II, Practicability of the Determinations, by Samuel E. Bailey. Pp. 1-10. October, 1908 ..... .10
2. (XXIV) The Leptomedusae of the San Diego Region, by Harry Beal Torrey. Pp. 11-31, with 11 text-figures. February, 1909 ..... .20
3. (XXV) The Ophiurans of the San Diego Region, by J. F. McClendon. Pp. 33-64, plates 1-6. July, 1909 ..... .30
4. (XXVI) *Halocynthia johnsoni* n. sp.: A comprehensive inquiry as to the extent of law and order that prevails in a single animal species, by Wm. E. Ritter. Pp. 65-114, plates 7-14. November, 1909 ..... .50
5. (XXVII) Three Species of *Cerianthus* from Southern California, by H. B. Torrey and F. L. Kleeberger. Pp. 115-125, 4 text-figures. December, 1909 ..... .10
6. The Life History of *Trypanosoma dimorphon* Dutton & Todd, by Edward Hindle. Pp. 127-144, plates 15-17, 1 text-figure. December, 1909 ..... .50
7. (XXVIII) A Quantitative Study of the Development of the Salpa Chain in *Salpa fusiformis-runcinata*, by Myrtle Elizabeth Johnson. Pp. 145-176. March, 1910 ..... .35
8. A Revision of the Genus *Ceratocorys*, Based on Skeletal Morphology, by Charles Atwood Kofoid. Pp. 177-187. May, 1910 ..... .10
9. (XXIX) Preliminary Report on the Hydrographic Work Carried on by the Marine Biological Station of San Diego, by George F. McEwen. Pp. 189-204; text-figure and map. May, 1910 ..... .15
10. (XXX) Biological Studies on *Corymorpha*. III, Regeneration of Hydranth and Holdfast, by Harry Beal Torrey. Pp. 205-221; 16 text-figures.
11. (XXXI) Note on Geotropism in *Corymorpha*, by Harry Beal Torrey. Pp. 223-224; 1 text-figure.

    Nos 10 and 11 in one cover. August, 1910 ..... .20
12. The Cyclostomatous Bryozoa of the West Coast of North America, by Alice Robertson. Pp. 225-284; plates 18-25. December, 1910 ..... .60
13. Significance of White Markings in Birds of the Order Passeriformes, by Henry Chester Tracy. Pp. 285-312. December, 1910 ..... .25
14. (XXXIII) Third Report on the Copepoda of the San Diego Region, by Calvin Olin Esterly. Pp. 313-352; plates 26-32. February, 1911 ..... .40
15. The Genus *Gyrocotyle*, and Its Significance for Problems of Cestode Structure and Phylogeny, by Edna Earl Watson. Pp. 353-468; plates 33-48. June, 1911 ..... 1.00

    Index, pp. 469-478.

* Roman numbers indicate sequence of the Contributions from the Laboratory of the Marine Biological Association of San Diego.

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY
Vol. 11, No. 6, pp. 127-142, pls. 3-4 August 30, 1913

PYCNOGONIDA FROM THE COAST OF CALIFORNIA

WITH DESCRIPTIONS OF TWO NEW SPECIES

BY
HARRY V. M. HALL

The following paper is based upon the collections of the University of California which include certain material from the Bay of San Francisco, and that collected by me during the summers of 1911 and 1912, at Laguna Beach, California, in connection with the Marine Laboratory of Pomona College. This collection from Laguna Beach, which I have donated to the Museum of the University of California, includes over sixty specimens, most of which belong to the commonest species, namely, *Ammothella bi-unguiculata* Dohrn var. *californica* Hall. Five other species in as many genera are also represented.

The habitat from which the specimens were taken admits of little generalization, owing to the varied character of the coast. Most of them were taken from the under sides of stones lying on sandy or gravelly bottom between tide marks, some from *Fucus* growing on rocky ledges or large stones, a few from red algae growing in rock-bound tide pools, and still others from among the bases of *Phyllospadix* which grows in the mud and sand at the extreme low tide mark. The whole coast is open to the surf in the vicinity of Laguna Beach, but is rather varied in structure. Rocky headlands of sandstone, some of it homogeneous and some a coarse conglomerate, furnish attachment for a great variety of animal and vegetable life, as do also the broken fragments of all shapes and sizes which strew some of the beaches between

the headlands. All such stones within two miles of headquarters that were small enough to be turned over, were turned from one to three times in the course of the summer; tide pools and crevices in the rocky beaches received a thorough and continued inspection as far down as the extreme low tide mark. Since several members of the party were interested in mites, isopods, nudibranch molluscs, collembola, and pycnogonids, it is evident that our search was minute and careful, as well as somewhat extensive.

We noticed in 1912 several apparent changes in the fauna of the coast since the preceding summer. Those changes in which a species showed an increase in numbers over the preceding year, are, of course, to be discounted by our increased experience and efficiency as collectors and by our better knowledge of the locality. On the other hand many forms which we had found to be fairly common the summer previous, were either very rare or apparently completely missing this year. Several Pycnogonida were taken that had escaped our notice the summer before and the notes on these descriptions of the two new species form the body of this paper.

The key to the Pycnogonida of the West Coast given in this paper is based on that given by Dr. Leon J. Cole (1904). My thanks are also due Dr. Cole for his kindly criticism and valued suggestions in connection with the preparation of this paper. Dr. Cole's type specimens were kindly loaned me for comparison by Professor C. A. Kofoid, and for this and many other favors my thanks are also due him. Dr. Cole's paper is based on the material collected by Professor W. E. Ritter, on the Harriman Alaska Expedition, a few specimens collected by Professor Trevor Kincaid on the Priblof Islands, and collections made at various points along the California coast by Dr. S. J. Holmes and others of the staff of the Department of Zoology of the University of California. The present paper is in a way supplementary to Dr. Cole's, and in it I have endeavored to bring the account of the Pycnogonida of the West Coast of North America up to date.

NOTES ON OCCURRENCE

Anoplodactylus californicus Hall

Plate 4, figs. 14, 15, 16

Described by me (see Hall, 1912, p. 91) from a single female specimen which was swept from *Fucus* at Laguna Beach, August, 1911. In the summer of 1912 we discovered that the usual habitat of this species at Laguna Beach is among the bases of the *Phyllospadix* which grows at the extreme low tide mark. At that time, July 16, 1912, we took several specimens of both sexes, thus permitting the presentation of figures showing the sexual dimorphism (figs. 14, 15, 16) and the completion of the description as follows.

Male one-fifth smaller than female, with six-jointed ovigers (fig. 16), the last three segments of which are spirally rolled and closely set with spines, most of which point proximally. Several globular masses of white eggs. Chelae of both sexes often bent in front of the proboscis. Eye-tubercle and abdomen or caudal segment project from their respective ends of the body at about the same angle, inclined but slightly from the perpendicular. A protuberance on disto-inferior aspect of second coxal joint about twice as long in male as in female (figs. 14, 15). Opening of the cement gland of male on superior aspect of femur one-third to one-half the way from coxae on legs II, III, and IV (fig. 15).

Measurements of *A. californicus* in Millimeters

	Type	Maximum		Minimum	
	♀	♂	♀	♂	♀
Length (approximate)	3.	3.3	3.6	3.	2.8
Proboscis	1.5	1.5	1.6	1.2	1.3
Body	1.5	1.8	2.1	1.7	1.5
Span of processes II	1.5	1.8	1.8	1.65	1.4
Caudal segment	.6	.53	.65	.4	.5
Leg III (approximate)	8.5	9.	10.2	7.1	8.7

The above measurements, as well as those that are given in the succeeding pages of this paper, are taken as follows: Length is the distance from tip of proboscis to tip of caudal segment, the animal being flattened for the purpose, or the measurement approximated; proboscis is the measurement from base to tip;

body is measured from base of proboscis to base of caudal segment; span of processes II is the distance measured across the body between the tips of leg-bearing processes of legs II; leg III is the approximate length of leg III, not including the leg-bearing process; to get the "extent" as used by Cole (1904), add twice the length of "leg III" to the "span of processes II". All measurements have been taken with an ocular micrometer. Slight inaccuracies in measurement given in my earlier pages (Hall, 1912, pp. 92–99) have been corrected in this paper.

Ammothella bi-unguiculata Dohrn var. **californica** Hall

Described by me (see Hall, 1912, p. 93) from twenty specimens taken at Laguna Beach, during July and August, 1911. Over fifty specimens of this species were taken in the summer of 1912 under stones in the same locality. Corrected measurements are given below.

Measurements of *A. bi-unguicuata* var. *californica* in Millimeters

	Type		Maximum		Minimum
	♀	♂	♀	♂	♀
Length	2.85	2.5	2.85	2.4	1.38*
Proboscis	1.15	.9	1.15	.96	.6
Body	1.35	1.15	1.35	1.2	.63
Caudal segment	.3	.24	.3	.25	.15
Span of Process II	.66	.75	.66	.45	.35
Leg III (approximate)	4.5	3.5	4.5	2.8	1.5

* Immature.

Ammothella spinosissima Hall

Described by me (see Hall, 1912, p. 95), from a single specimen which was swept from *Fucus*, July, 1911, at Laguna Beach. During the summer of 1912 two specimens of this species were taken, one under a stone, the other swept from *Fucus*. These specimens differ so little in size from the type that I give the type measurements only, in millimeters, as follows: Length 3.6; proboscis 1.35; body 1.5; caudal segment 1.05; span of processes II–1.8; legs III (approximate) 7.

Lecythorhynchus marginatus Cole

Described by Cole (1904, p. 260). Two specimens of this species were taken from red algae in a tide pool, at Laguna Beach, July 17, 1912.

Tanystylum intermedium Cole

Described by Cole (1904, p. 278). Three specimens of this species were taken, two from algae in a tide pool and one from under side of a stone, at Laguna Beach, July 9, and August 13, 1912.

Pallene californiensis sp. nov.

One specimen of this species was taken under a stone about half way between tide marks, at upper end of the channel at Coward's Cove, Laguna Beach, August 15, 1912. This is the first representative of this genus or family to be reported from the Pacific Coast of North America.

KEY TO THE PYCNOGONIDA OF THE WEST COAST

A. Oviger 10- or 11-jointed; the first three joints short, sub-equal in size; distal segments spirally rolled, with one to three rows of denticulate spines.
  B. Chelifori powerful; chelae lying before the mouth; palpi wanting or represented in male only by a 1- to 4-jointed stub.....Family **Pallenidae**
    C. Spines on terminal segment of oviger rounded at tip; often broad distally, never pointed, always finely toothed; last two body-segments usually grown together; with auxiliary claws; chelae finely toothed; oviger usually without terminal claws.....Genus **Pallene**
      D. Body very compact; leg-bearing processes with bases contiguous; proboscis three-fourths its own diameter in length.....**P. californiensis,** n. sp.

AA. Oviger with ten or fewer joints; first three joints not so much smaller than the following joints; distal joints less developed or wanting; several feathered spines on distal segments but not arranged in rows.
  B. Chelifori present, not chelate in adult; palpi present; ovigera 10-jointed, present in both sexes.....Family **Ammotheidae**
    C. Body elongate, distinctly segmented; lateral processes well separated; chelifori 1-jointed; palpi 9-jointed.....Genus **Lecythorhynchus**
      D. Proboscis subcylindrical or elliptical, constricted in its middle third.....**L. marginatus** Cole
    C'. Body more or less disciform; segmentation often indistinct; lateral processes approximated.

D. Chelifori 2- or 3-jointed; palpi 8- or 9-jointed.
E. Chelifori 2-jointed; palpi 8-jointed.....Genus **Ammothea**
F. Chelifori more than half as long as the proboscis; caudal segment reaching at least to middle of second coxal joint of fourth pair of legs..**A. latifrons** Cole
F′. Chelifori less than half as long as proboscis.
G. Proboscis narrow, fusiform; forms less than 4 mm. in length and 20 mm. in extent.
H. Protuberance on dorsal side of first coxal joint about half as long as the joint; genital protuberance in male about the same length .....**A. alaskensis** Cole
H′. Protuberance on dorsal side of first coxal joint fully three-fourths as long as the joint; genital protuberance in male only about half as long as protuberance on first coxal joint .....**A. gracilipes** Cole
H″. Protuberance on dorsal side of first coxal joint less than half as long as the joint, short and blunt; no protuberance on lateral processes; no triangular projection on disto-dorsal aspect of first joint of chelifore. Female larger than male.....**A. nudiuscula** sp. nov.
G′. Proboscis broadly clavate, truncate at apex; forms over 4 mm. in length and 20 mm. in extent .....**A. pribilofensis** Cole
E′. Chelifori 3-jointed; palpi 9-jointed..Genus **Ammothella**
F. Eye tubercle low, rounded.
G. First two or three trunk segments with a conical tubercle dorsally near the posterior border.....**A. tuberculata** Cole
G′. No tubercle dorsally in such position; terminal claw very rudimentary; auxilliary claws greatly developed; from California coast.....**A. bi-unguiculata** Dohrn var. **californica** Hall
F′. Eye tubercle tall, slender; caudal segment slender, curved, elevated, spinose.
G. First and second trunk segments with a pair of spines dorsally near the posterior border; no spine-bearing processes on dorsum, nor on tibial joints.....**A. spinifera** Cole
G′. Three spine-bearing processes on dorsum; two rows of spine-bearing processes along the dorsal margin of tibial joints.....**A. spinosissima** Hall
D′. Chelifori usually 1-, sometimes 2-jointed; palpi 6- or 7-jointed.....Genus **Tanystylum**
E. Chelifori 2-jointed.....**T. intermedium** Cole
D″. Chelifori 1-jointed; palpi 4-jointed; body very much shortened.....Genus **Clotenia**—**C. occidentalis** Cole

B′. Chelifori present, chelate; palpi absent; ovigera present in male only, 5- or 6-jointed.....Family **Phoxichilidiidae**

C. First trunk segment produced very little, or not at all, anteriorly beyond base of proboscis; lateral processes well separated; ovigera 5-jointed.....Genus **Phoxichilidium—P. femoratum** Cole

C′. First trunk segment projecting somewhat anteriorly beyond base of proboscis; body concentrated, lateral processes closely approximated.....Genus **Halosoma—H. viridintestinalis** Cole

C″. First trunk segment projecting well beyond base of proboscis, forming a slender neck; body usually elongate, lateral processes usually well separated; ovigera 6-jointed.....Genus **Anoplodactylus**

D. Caudal segment directed upward; lateral processes well separated at the bases.....**A. erectus** Cole

D′. Lateral processes contiguous at the bases.....**A. californicus** Hall

B″. Chelifori and palpi both absent; ovigera present in the male only.....Family **Pycnogonidae**

C. Ovigera 9- or 10-jointed.....Genus **Pycnogonum**

D. Ovigera 10-jointed.....**P. stearnsi** Ives

DESCRIPTIONS OF NEW SPECIES

Pallene californiensis sp. nov.

Pl. 4, figs. 9–13

Type ♀, in University of California collection, Laguna Beach, Orange County, California, August 15, 1912, collected by H. V. M. Hall.

Description.—Body short, stout; surface smooth; anterior corners of the first body segment rounded, a considerable gradual constriction of this joint laterally half way between posterior border of segment and base of chelifori. Lateral (leg-bearing) processes with bases contiguous. A furrow in the integument makes them appear almost like a pre-coxal joint of the legs (fig. 9). Segmentation distinct between first and second, and second and third body segments. Third and fourth body segments united, but with a line or furrow in the integument across the body anterior to insertion of caudal segment that shows trace of obsolete segmentation between these segments.

Proboscis very short and blunt; length about three-fourths its own diameter; anterior corners rounded (fig. 10).

No eyes apparent; eye tubercle low, situated above and between lateral processes of legs I, distant about its own diameter from posterior border of segment (fig. 11).

Caudal segment short, with very little elevation; anus in a notch at the end. Length of caudal segment about equal to its own diameter, or to length of coxa I of leg IV; inserted above the fourth body segment, its anterior end marking the division between body segments three and four.

Chelifori stout; chelae finely dentate; shaft short, length one and one-half times its own diameter, shorter than chelae; proximal to shaft the basal segments of the two chelifori appear grown together forming a transverse ridge anteriorly above the proboscis and extending forward over half the length of the latter (figs. 10, 11).

Palpi wanting.

Oviger 10-jointed; the four terminal joints spirally rolled and with a row of flat denticulate spines on inside edge of spiral. No terminal claw; first three joints very short; fourth about as long as first three together; fifth joint the longest, with a protuberance on distal end directed opposite to spiral of terminal joints, as high as three-fourths of joint. Two simple curved hairs, one at tip of protuberance and the other distally and at the base of same. Terminal five joints short and sub-equal in length, their diameter diminishing slightly in order (fig. 13).

Legs rather slender, no protuberances evident; first coxae about as long as their own diameters; coxae II about three times as long and slightly clavate; coxae III about one and one-half times the length of coxae I. Femora about equal in length to combined length of coxae I, II, and III. First tibial joints not quite as long as femora; second tibial joints about as long as femora, but with slightly smaller diameter. Tibial joints with scattering hairs. Tarsus (fig. 12) a little less than half as long as second tibial joints. Terminal claws a little over half the length of tarsus. Auxiliary claws two-thirds as long as terminal claws. Several simple hairs on distal end of tarsus. Spines on "sole" are very stout, especially so near the "heel". A sparse

fringe of hairs usually apparent at the distal end of each joint in all the legs (fig. 9).

Color pale straw, no markings in color. Measurements (in millimeters); length 1.25; proboscis 0.27; body 0.93; caudal segment 0.15; span of processes II, 0.6; leg III (approximately), 4.05.

Remarks.—One specimen, a female, was taken under a stone half way between tide marks. The species is apparently rather rare, for our seach for Pycnogonida living under stones was very careful and was continued all summer, every time the tide was low enough for collecting. This is the first member of the genus and family to be reported from the Pacific Coast.

Comparisons.—General form of the body somewhat similar to that of *Pallene laevis* Hoek (1881, p. 78). The proboscis is not pointed nor is it nearly as long as that of *P. laevis*, nor does the oviger end in a claw in my species. The proboscis is more like that of *Pallene empusa* Wilson (1878, p. 476). The general shape of body segment I is much stouter than in *P. empusa* and many other features distinguish the two species.

Ammothea nudiuscula, sp. nov.

Pl. 3, figs. 1–8

Type ♂ and ♀, in University of California collection, Key Route Pier, San Francisco Bay, March 27, 1912, collected by G. E. Stone among hydroids and bryozoans.

Description.—Body short, stout; surface pitted but not deeply nor closely so; segmentation indistinct; anterior corners of first body segment rounded; lateral (leg-bearing) processes grown together for nearly their whole length (figs. 1, 4).

Proboscis about the length of the body as far back as the base of caudal segment; spindle-shaped, with rounded anterior corners between which is a vertical notch; not depressed to any extent in either sex, largest diameter half way from base to tip; no constriction on distal half. Side view (fig. 2) shows upper side of proboscis more convex than lower side. Transverse diameter of proboscis about half its length in the male, vertical diameter a little less than transverse. Proboscis of female rather broader than that of male.

Eye tubercle low with four black eyes; tubercle does not project over the proboscis (figs. 1, 4).

Caudal segment with very little elevation, projecting almost directly back; length about three times its transverse diameter. In male it reaches to end of coxa I of leg IV. In female it reaches almost half way down coxa II of leg IV (figs. 1, 2, 4).

Chelifori small, 2-jointed, with globular terminal joint and stout shaft; no chelae. They extend about one-third the length of proboscis; two short spines on disto-inferior corner of first joint of chelifore (figs. 1, 4).

Palpi 8-jointed; first joint short and stout, second about the length of chelifori, third short, fourth about the length of second, terminal joints short and decreasing in order; on last joints are a few short spines, none longer than diameter of terminal joint. Male palpus with three other spines, one on tip of second, third and fourth joints (figs. 1, 4).

Oviger 10-jointed, bent like a hook, not spirally rolled. That of male about twice the length of palpus and bearing several bunches of dark-colored eggs. Several apparently simple spines on terminal joints. First joint short and stout. The rest numbered in order of length: 3, 4, 5, 2, 6, 7, 8, 9, 10. Oviger of female about the same length as palpus; few hairs on terminal joints, some of them compound; joints numbered in order of length: 5, 4, 2, 3, 6, 1, 7, 8, 9, 10 (figs. 3, 7).

Legs of male rather slender, with more spines than in other sex. First coxal joint of all legs about as broad as long, with blunt spurs on disto-superior aspect. Coxae II constricted at base, almost twice as long as coxae I. Coxae II of legs III and IV have blunt protuberance on disto-inferior corner. Coxae III slightly longer than and not so thick as coxae I. Femora about the same diameter as coxae I, and about as long as combined lengths of coxae I, II, and III. All the femora have blunt projections on disto-superior corners, those on femora of legs II and IV with hairs at tip. Tibial joints about the same length as femora but with slightly smaller diameter. Tarsus not quite three-fourths the length of tibial joints. Terminal claws about one-half the length of tarsus. Auxiliary claws three-fourths the length of terminal claws. On the "sole" or tarsus at the "heel"

are three or four stout spines, while the rest of the spines on the "sole" are short, fine, and often not apparent (figs. 1, 2, 5).

Legs of female similar except in following particulars: appearance much stouter than those of male on account of the femora, which are swollen with ova. Blunt spurs, similar to those on coxae I of male, occur in similar positions on coxae I of legs II and III in female. Coxa II is one and one-half times the length of coxa I; it is constricted at the base and is without projections. Femora are swollen to almost twice the diameters of coxae I, slightly longer than combined lengths of coxae I, II, and III; with slight rounded spurs on disto-superior corner. Tibial joints not quite so long as, and about half the diameter of, the femora (figs. 4, 5).

Color straw, eyes and eggs black.

Measurements of *A. nudiuscula* in Millimeters

	Type ♂	Type ♀
Length	1.86	2.12
Proboscis	0.72	0.87
Body	1.	0.74
Caudal segment	0.1	0.51
Span of processes II	0.93	0.9
Leg III (approximate)	3.69	4.22

Remarks.—Two specimens, one male and one female, were kindly loaned me by Professor C. A. Kofoid of the University of California. They were taken from *Tubularia* on piling of the Key Route Wharf in San Francisco Bay, March 27, 1912.

Comparisons.—This species is nearest to *Ammothea alaskensis* Cole but differs in the following particulars: no protuberances on leg-bearing processes; no spines on caudal segment; no constriction on distal half of proboscis; no triangular projection distally on dorsal side of first joint of chelifore, but instead two bristles distally on ventral side of same; protuberance on coxae I not by any means "long and slender"; no row of slender bristles along dorsal curve of tarsus apparent; female one-seventh *larger* than male instead of "slightly smaller" than male, as in *A. alaskensis;* on the whole a much less hairy species than any of this genus hitherto described from the Pacific Coast of North America.

LITERATURE CITED

Cole, L. J.
1904. Pycnogonida of the West Coast of North America. Harriman Alaska Expedition, **10**, 247–298, pls. 11–26.

Hall, H. V. M.
1912. Studies in Pycnogonida I. Rep. Laguna Mar. Lab., **1912**, 91–99, figs. 49–52 in text.

Hoek, P. P. C.
1881. Report on the Pycnogonida dredged by H. M. S. Challenger during the years 1873–76. Zool. Chall. Exp., part X, 1–167, pls. 1–15.

Loman, J. C. C.
1908. Die Pantopoden der Siboga-Expedition. Resultats Siboga-Expeditie, **40**, 1–87, pls. 1–15.

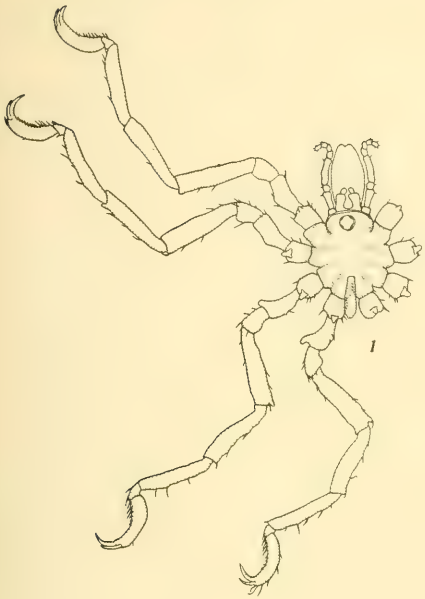
Wilson, E. B.
1878. Report on the Pycnogonida of New England and adjacent waters. Rep. U. S. Fish Comm., **6**, 463–506, pls. 1–7.

EXPLANATION OF PLATES

PLATE 3

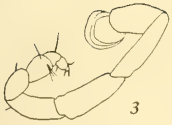
Ammothea nudiuscula

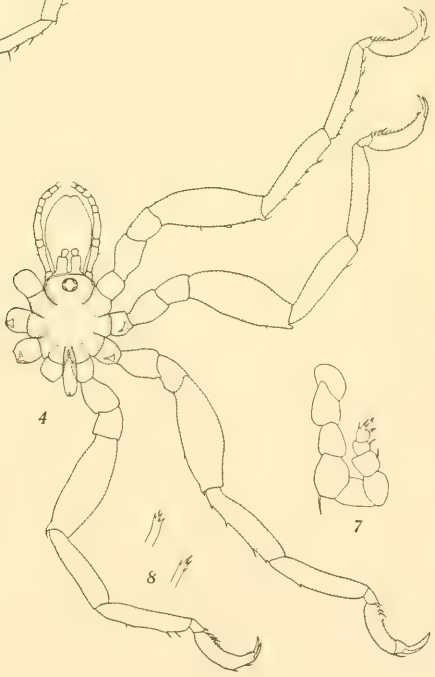
Fig. 1. Male from above. × 16.
Fig. 2. Male from left side. × 18.
Fig. 3. Male, left oviger from below. × 35.
Fig. 4. Female from above. × 16.
Fig. 5. Female, tarsus of left leg I. × 35.
Fig. 6. Female, right palpus and chelifore. × 35.
Fig. 7. Female, right oviger from below. × 35.
Fig. 8. Female, hairs from last two segments of right oviger. × 150.


1

6

2


3


4

7

5

8

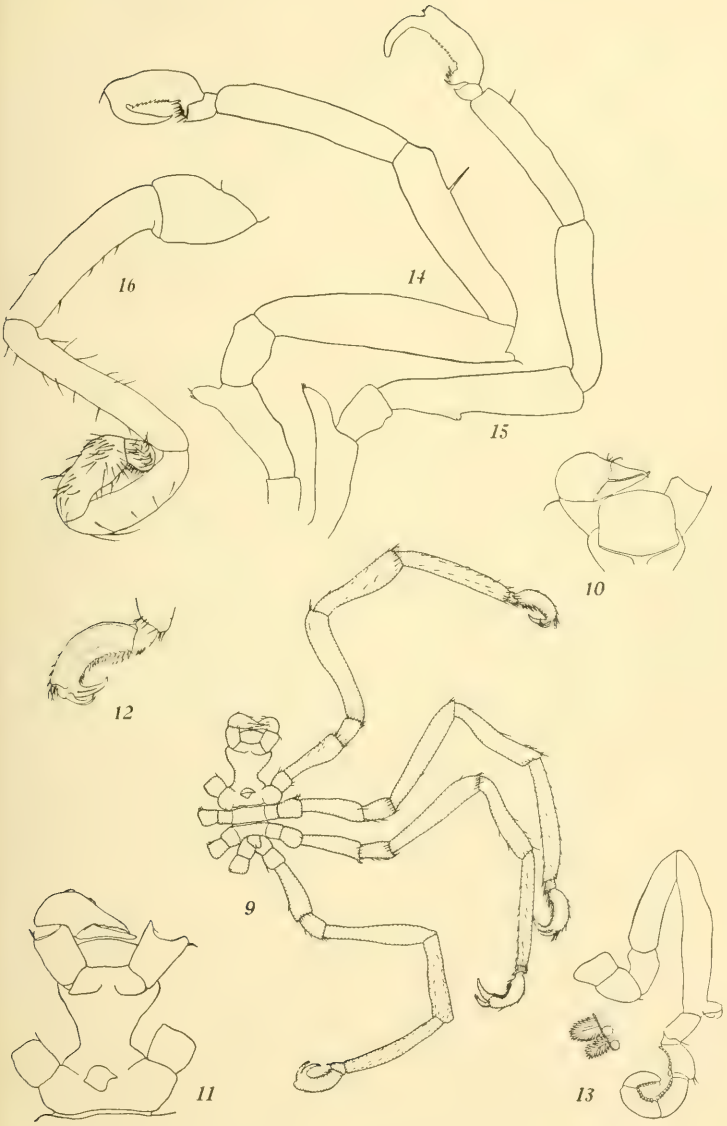
PLATE 4

Pallene californiensis

Fig. 9. Female from above. × 17.
Fig. 10. Proboscis and chelifore from below. × 35.
Fig. 11. Proboscis, chelifore and first body segment from above. × 35.
Fig. 12. Tarsus of left leg I. × 43.
Fig. 13. Left oviger from below, × 43, and two of the denticulate spines greatly enlarged.

Anoplodactylus californicus

Fig. 14. Female, left leg IV. × 18.
Fig. 15. Male, left leg IV. × 18.
Fig. 16. Male, right oviger from below. × 43.


16
14
15
10
12
9
11
13

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY
Vol. 11, Nos. 7 and 8, pp. 143-172, pls. 5-8 September 24, 1913

OBSERVATIONS ON ISOLATED LIVING PIGMENT CELLS FROM THE LARVAE OF AMPHIBIANS

BEHAVIOR OF ECTODERMIC EPITHELIUM OF TADPOLES WHEN CULTIVATED IN PLASMA

BY
S. J. HOLMES

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY

Smithsonian Institution
OCT 16 1913
National Museum

UNIVERSITY OF CALIFORNIA PUBLICATIONS

Note.—The University of California Publications are offered in exchange for the publications of learned societies and institutions, universities and libraries. Complete lists of all the publications of the University will be sent upon request. For sample copies, lists of publications or other information, address the Manager of the University Press, Berkeley, California, U. S. A. All matter sent in exchange should be addressed to The Exchange Department, University Library, Berkeley, California, U. S. A.

OTTO HARRASSOWITZ, LEIPZIG.

Agent for the series in American Archaeology and Ethnology, Classical Philology, Education, Modern Philology, Philosophy, Psychology, History.

R. FRIEDLAENDER & SOHN, BERLIN.

Agent for the series in American Archaeology and Ethnology, Botany, Geology, Geography, Mathematics, Pathology, Physiology, Zoology, and Memoirs.

ZOOLOGY.—W. E. Ritter and C. A. Kofoid, Editors. Price per volume, $3.50. Commencing with Volume II, this series contains Contributions from the Laboratory of the Marine Biological Association of San Diego.

Cited as Univ. Calif. Publ. Zool.

Volume 1, 1902-1905, 317 pages, with 28 plates $3.50

Volume 2 (Contributions from the Laboratory of the Marine Biological Association of San Diego), 1904-1906, xvii + 382 pages, with 19 plates $3.50

Volume 3, 1906-1907, 383 pages, with 23 plates $3.50

Volume 4, 1907-1908, 400 pages, with 24 plates $3.50

Volume 5, 1908-1910, 440 pages, with 34 plates $3.50

Vol. 6.

1. (XXIII) On the Weight of Developing Eggs. Part I, The Possible Significance of Such Investigations, by William E. Ritter; Part II, Practicability of the Determinations, by Samuel E. Bailey. Pp. 1-10. October, 1908 ..... .10
2. (XXIV) The Leptomedusae of the San Diego Region, by Harry Beal Torrey. Pp. 11-31, with 11 text-figures. February, 1909 ..... .20
3. (XXV) The Ophiurans of the San Diego Region, by J. F. McClendon. Pp. 33-64, plates 1-6. July, 1909 ..... .30
4. (XXVI) *Halocynthia johnsoni* n. sp.: A comprehensive inquiry as to the extent of law and order that prevails in a single animal species, by Wm. E. Ritter. Pp. 65-114, plates 7-14. November, 1909 ..... .50
5. (XXVII) Three Species of *Cerianthus* from Southern California, by H. B. Torrey and F. L. Kleeberger. Pp. 115-125, 4 text-figures. December, 1909 ..... .10
6. The Life History of *Trypanosoma dimorphon* Dutton & Todd, by Edward Hindle. Pp. 127-144, plates 15-17, 1 text-figure. December, 1909 ..... .50
7. (XXVIII) A Quantitative Study of the Development of the Salpa Chain in *Salpa fusiformis-runcinata*, by Myrtle Elizabeth Johnson. Pp. 145-176. March, 1910 ..... .35
8. A Revision of the Genus *Ceratocorys*, Based on Skeletal Morphology, by Charles Atwood Kofoid. Pp. 177-187. May, 1910 ..... .10
9. (XXIX) Preliminary Report on the Hydrographic Work Carried on by the Marine Biological Station of San Diego, by George F. McEwen. Pp. 189-204; text-figure and map. May, 1910 ..... .15
10. (XXX) Biological Studies on *Corymorpha*. III, Regeneration of Hydranth and Holdfast, by Harry Beal Torrey. Pp. 205-221; 16 text-figures.
11. (XXXI) Note on Geotropism in *Corymorpha*, by Harry Beal Torrey. Pp. 223-224; 1 text-figure.

    Nos 10 and 11 in one cover. August, 1910 ..... .20
12. The Cyclostomatous Bryozoa of the West Coast of North America, by Alice Robertson. Pp. 225-284; plates 18-25. December, 1910 ..... .60
13. Significance of White Markings in Birds of the Order Passeriformes, by Henry Chester Tracy. Pp. 285-312. December, 1910 ..... .25
14. (XXXIII) Third Report on the Copepoda of the San Diego Region, by Calvin Olin Esterly. Pp. 313-352; plates 26-32. February, 1911 ..... .40
15. The Genus *Gyrocotyle*, and Its Significance for Problems of Cestode Structure and Phylogeny, by Edna Earl Watson. Pp. 353-468; plates 33-48. June, 1911 ..... 1.00

    Index, pp. 469-478.

*Roman numbers indicate sequence of the Contributions from the Laboratory of the Marine Biological Association of San Diego.

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY

Vol. 11, No. 7, pp. 143-154, pls. 5-6 September 24, 1913

OBSERVATIONS ON ISOLATED LIVING PIGMENT CELLS FROM THE LARVAE OF AMPHIBIANS

BY
S. J. HOLMES

It has long been a mooted question whether the movement of pigment in chromatophores is due to the change in outline of the cell itself, or to the flow of pigment within cell processes which remain comparatively constant in form. Brücke (1852) in his classical memoir on the color changes of the chameleon was among the first to champion the latter view, and since his time the majority of workers who have carefully studied the movements of chromatophores in vertebrates have come to the same opinion. Virchow, Harless, von Wittich, Lister, Ehrmann, and Gaupp have ascribed the color changes in amphibians to movements of pigment within the cell. Biedermann (1892) in his thorough paper on the color changes of *Hyla* describes processes of the chromatophores devoid of pigment, but he leaves the question open as to the method of pigment distribution. While pigment may be withdrawn from and extend into the cell processes, the latter may nevertheless, according to Biedermann, be capable of amoeboid movement. H. Müller (1860) likewise takes an undecided position on account of the difficulty of deciding between the alternative views.

The versatile histologist Leydig (1876), on the other hand, regarded the amphibian melanophores as amoeboid cells, a view more recently defended by Ficalbi (1896) and by Galovine (1907).

Similar differences on this point occur among workers on the chromatophores of fishes, reptiles and various invertebrates. Loeb's (1899) observations on the migration of pigment cells in the yolk sac of *Fundulus* indicated that these cells were amoeboid, as Heincke (1880) considered them to be in *Gobius* and *Syngnathus*. Ballowitz (1893) finds that in the herring the terminal cell processes of the retracted melanophores are free from pigment, and he concludes that there is no amoeboid movement of the cells, but only "ein Ausströmen und Zurückströmen der Pigmentkörnchen in dem unverändert liegen bleibenden Protoplasma." Zimmermann (1893) and Solger (1890) maintain the same view, and Franz (1908) who studied the movements of pigment cells in the fins of various young fishes where they can be seen with exceptional clearness in the living animal, attributes the greater part of the changes to movements of granules within the cell, although he does not deny that changes in the outline of the cell may occur.

The foregoing may perhaps suffice to indicate the state of opinion regarding the movements of chromatophores in the vertebrates. A general discussion of the literature of the subject will not be attempted, especially since it has recently been reviewed by van Rynberk (1906). I may mention, however, an observation made more or less incidentally by Harrison (1910) in the course of his valuable investigations on the outgrowth of nerve fibres from the neuroblasts of frog embryos. Pigment was observed to increase in some of the cells of a frog embryo that were kept in lymph, and "the individual cells changed slightly in form". The changes in one cell were sketched at intervals of two or three days. Harrison's account rather implies that these cells were not isolated from the surrounding tissue, and the relation of the pigment to the processes of the cell was not described.

While studying the behavior of small pieces of the embryos and larvae of *Hyla regilla* when cultivated in hanging drops of blood plasma or serum, I observed that the pigment cells sometimes wandered away from the rest of the tissue and became entirely isolated. Epithelial cells and connective tissue corpuscles were frequently seen to behave in a similar manner, especially

when they happened to come in contact with the cover slip from which the culture was suspended. Sometimes the connective tissue cells migrated out along the surface film of the lower side of the drop, but in no case were the pigment cells observed to creep outward unless they came into contact with the glass. The isolated position of the pigment cells presents an exceptionally favorable opportunity for the study of their structure and movements. While these cells are in their natural situation within the tissues of the body it is often possible to see very clearly the distribution of their pigment, but next to impossible in most cases to follow the outlines of the cells themselves. The uncertainty that has so long prevailed in regard to the movements of chromatophores is largely the result of this difficulty. When the pigment cells accommodatingly isolate themselves, and get out where one can get a good look at them with all powers of the microscope, and then exhibit characteristic changes in the distribution of their pigment, the difficulties of observation are practically all cleared away.

The observations on *Hyla* were made upon embryos nearly ready to come out of the jelly, and upon larvae that had recently emerged. After a short treatment with weak hydrogen peroxide solution (a stronger one is soon fatal) the embryos or larvae were placed in sterile Ringer's solution and cut into small pieces. A single piece was then placed in a hanging drop of the culture medium, and sealed up in a hollow slide. Pieces put up in Ringer's or Locke's solution, while they lived several days and showed more or less outwandering of cells, failed to afford any good cases of active migration of chromatophores, nor did the chromatophores while in the tissues present as natural and healthy an appearance after a few days as pieces put up in plasma or serum. Owing probably to the weak antiseptic solutions that could be used without injuring the animals, preparations in Ringer's or Locke's solutions were frequently infected by bacteria, while such contamination was much less common in preparations made with fluids from the blood.

Preparations in plasma showed in several cases, but by no means in all, a wandering out of a few pigment cells from one to three days after being mounted. The different pigment cells

that migrated out manifested a remarkable diversity. Some were oval with a few short processes; some were long and narrow; some had a few very long and slender processes, and others had many branches. By watching a single chromatophore it was easy to see that it changed in form, in many respects, like an amoeba. Processes were protruded here and drawn in there, so as to produce within a very few minutes marked changes in outline. Figures 4–8 (pl. 5) illustrate successive changes in form of the same cell that were undergone within a half hour. Figures 2 and 3 represent in more detail the same cell at different times. A single nucleus could be seen near the center of each chomatophore when not too deeply overlaid with granules.

In the melanophores there is a thin outer layer of protoplasm of excessive transparency, so that it requires careful observation even under the ideal conditions that were afforded, in order to follow its course. It would be quite impossible to detect this material when surrounded by other tissues. Within this outer layer is a more fluid endoplasm which contains the melanin pigment.

The layer of ectoplasm is not a mere membrane that functions passively, but an active layer like the ectoplasm of a common amoeba, which it resembles in its mode of behavior. Where a process of the pigment cell is to be formed, the ectoplasm becomes thickened, then extends, usually as a narrow strand. Soon the more fluid endoplasm invades the process, as in ordinary amoeboid motion, carrying with it the granules of pigment. Processes may continue to extend in one direction many times the diameter of the cell. Usually they are narrow, but occasionally there may be broader sheets of protoplasm put forth which are at first comparatively free from granules, but they are generally invaded before long with more pigment. In an advancing pseudopod the ectoplasm is thin, except at the tip, and comparatively uniform. When the pseudopod is withdrawn the ectoplasm becomes broader and often more uneven in outline.

Frequently the branches of the chromatophore may meet and fuse. There is established in such cases a perfectly free communication between the endoplasmic contents of the two

branches. Several times I have watched the formation, meeting and fusion of cell processes, and have seen pigment granules flow freely past the point of union. A large cell may form in this way a considerable network of anastomosing branches.

The line separating endoplasm and ectoplasm is fairly sharp. The endoplasm, aside from the pigment granules, is not so transparent as the ectoplasm. It frequently contains remnants of yolk spherules in the central part of the cell. The pigment is in the form of small round black granules of nearly uniform size. In the narrower processes of the cell the granules are frequently constrained to pass single file, and sometimes a group of them may get wedged together and block the flow, leaving a stretch of the process free from pigment.

Processes of any considerable size devoid of pigment were not seen. The endoplasm with its pigment granules follows so closely the outpushings of the ectoplastic layer that the formation of a new branch of the cell makes very little headway before it is invaded by pigment. In all the free chromatophores observed the outline of the pigmented area gave a very faithful picture of the outline of the cell.

The amount of pigment in the chromatophores varied greatly. Some cells were densely crowded with black granules; others contained but very few. In fact every gradation occurred between very dark pigment cells and wandering cells which were probably destined to form connective tissue. Melanin granules occurred also in various other kinds of cells, especially the outer cells of the ectoderm.

Despite many attempts to obtain free pigment cells there were only a relatively few preparations in which these cells isolated themselves from the surrounding tissue. The melanophores from older larvae apparently lose some of their power of migration, partly perhaps on account of their greater complexity. As the larvae grow older the branches of the pigment cells become more numerous; anastomoses of the branches are more frequent, and it is doubtless more difficult for the cell, should it retain its power of amoeboid movement, to escape from its confinement among the other cells. Teasing up the tissue of older larvae in order to facilitate the isolation of the chromatophores gave only negative results.

A sharply defined beam of light was focused on some of the processes of the melanophores, but no clear evidence could be obtained that the light tended to make the process contract, even with long exposure. Even strong light, when the heat rays were filtered out, had little effect on the cell as a whole. A higher temperature increased the general activity of the cell. A warm needle placed immediately above the tip of a pseudopod would cause the ectoplasm to thicken and the pseudopod to be withdrawn more or less, but no very decided movements of the cell could be evoked by the local application of thermal stimuli. I have tried to direct the migration of the cell, by placing the tip of a heated needle over the pseudopods of one side, but met with no success. While the cells were quite active, and changed their form with considerable facility, they seemed to be lacking in the ability to get away from injurious stimulation. The pseudopods would make but little response even if the heat applied was sufficient to injure the protoplasm. Experiments upon stimulating the pigment cells could not be carried on as extensively as was desired on account of paucity of material. It would be of interest to determine the effect of various chemicals on the movements of the cells, but no work on this subject was attempted.

A few of the early stages in the development of the yellow pigment cells were isolated. One of them is shown in figure 10 (pl. 6). This cell contained a small amount of yellow pigment and several yolk granules. It showed a distinct amoeboid movement. A few minutes after it was sketched it had assumed the form shown in figure 11 (pl. 6). The attempt was made to stimulate one end of it by a hot needle applied to the cover slip, but the heat was too great and caused the cell to contract suddenly into an almost spherical form in which it remained (pl. 6, fig. 12). This cell showed a much greater contractility than the melanophores. Older yellow cells that were observed in small pieces of living tissue contained more abundant pigment: they were often irregularly branched, but the branches were thicker than those of the melanophores: In the larvae of *Diemyctylus torosus* the yellow cells are large and beautifully branched. The branches are fairly uniform in diameter and end bluntly, and they do not anastomose so freely as do those of the melanophores.

Where it is possible to find various stages between well-developed melanophores and xanthophores and the simple amoeboid cells of the embryonic mesoderm that go to form connective tissue, the well-developed chromatophores are not mere pigment-containing connective tissue corpuscles. The connective tissue corpuscles of a young larva of *Diemyctylus*, for instance, are different in form and mode of branching from any of the true pigment cells. Figure 15 shows a typical connective tissue cell from the thin part of the tail of a *Diemyctylus* larva. The branches of these cells are tapering and acute instead of nearly uniform and blunt as in the xanthophores. They are less numerous, less attenuated, and much less branched than those of the melanophores, and they do not often anastomose. The three types of cell are not connected in the older larvae by intermediate forms, but all of them represent diverging lines of development from a common amoeboid cell.

While the observations here recorded made it absolutely certain that the black and yellow pigment cells of young *Hyla* larvae have an amoeboid movement, it is of course possible that in the adult the cell processes of the chromatophores are more fixed in outline, and that the changes in the distribution of pigment may be brought about largely by the flow of granules within the cell. The extent to which amoeboid movements occur in the pigment cells of the larva, however, should render one somewhat skeptical regarding the commonly received interpretation of the pigment changes in the adult animal.

BIBLIOGRAPHY

Ballowitz, E.
1893. Ueber die Bewegungserscheinungen der Pigmentzellen. Biol. Zent., **13**, 625–630.

Biedermann, W.
1892. Ueber den Farbenwechsel der Frösche. Arch. ges. Physiol., **51**, 455–508, pl. 11.

Brücke, E.
1852. Untersuchungen über den Farbenwechsel des africanischen Chamäleons. Denksch. math.-naturw. Klasse d. k. Akad. Wiss., Wien., **4**, 179–210.

Ficalbi, E.
1896. Richerche sulla struttura minuta della pelle degli anfibi. Atti della R. Acad. Peloritana in Messina. Anno 11, 4 pls.

Franz, V.
1908. Die Struktur der Pigmentzelle. Biol. Zent., **28**, 536–548, 13 figs. in text.

Galovine, E.
1907. Études sur les cellules pigmentaires des vertébrés. Ann. Inst. Pasteur, **21**, 858–881.

Harrison, R. G.
1910. The outgrowth of the nerve fiber as a mode of protoplasmic movement. Jour. Exp. Zool., **9**, 878–848, pls. 1–3.

Heidenhain, M.
1911. Plasma und Zelle (Jena, Fischer), Bd. 1, Lief. 2, viii + 506, 276 figs. in text.

Heincke, F.
1880. Die Gobiidae und Syngnathidae der Ostsee nebst biologischen Bemerkungen. Arch. f. Naturgesch., **46**, 301–354, 1 fig. in text.

Leydig, F.
1876. Ueber die allgemeinen Bedeckungen der Amphibien. Arch. f. mikr. Anat., **12**, 119–242.

Loeb, J.
1899. On the heredity of the marking in fish embryos. Biological Lectures, Marine Biol. Lab. of Woods Hole, **1899**, 227–234, 6 figs. in text

Müller, H.
1860. Bewegungserscheinungen in ramifizierten Pigmentzellen in der Epidermis. Würzburger naturwiss. Zeit., **1**, 164–166.

Rynberk, G. van
1906. Ueber den durch Chromatophoren bedingten Farbenwechsel der Tiere (sog. chromatische Hautfunktion). Ergebnisse der Physiol., **5**, 347–571.

Solger, B.
1890. Ueber pigmentierte Zellen und deren Zentralmasse. Mitth. naturwiss. Vereins Neuvorpommern und Rügen, **22**, 1–34.

Zimmerman, K. W.
1893. Studien über Pigmentzellen. Arch. mikr. Anat., **41**, 367–389, pls. 23, 24.

EXPLANATION OF PLATES

PLATE 5

Fig. 1. Isolated melanophore from a young larva of *Hyla regilla; a*, enlarged portion of a fine pseudopod.

Figs. 2 and 3. A melanophore of *Hyla* drawn at different times.

Figs. 4, 5, 6, 7, 8. Successive stages in the changes of a single melanophore of a *Hyla* larva. All the changes figured occurred within a half hour.

Fig. 9. A large melanophore from the tail of a larva of *Diemyctylus*. The pseudopods show numerous anastomoses.

4
6
7
5
3
8
1
2
a

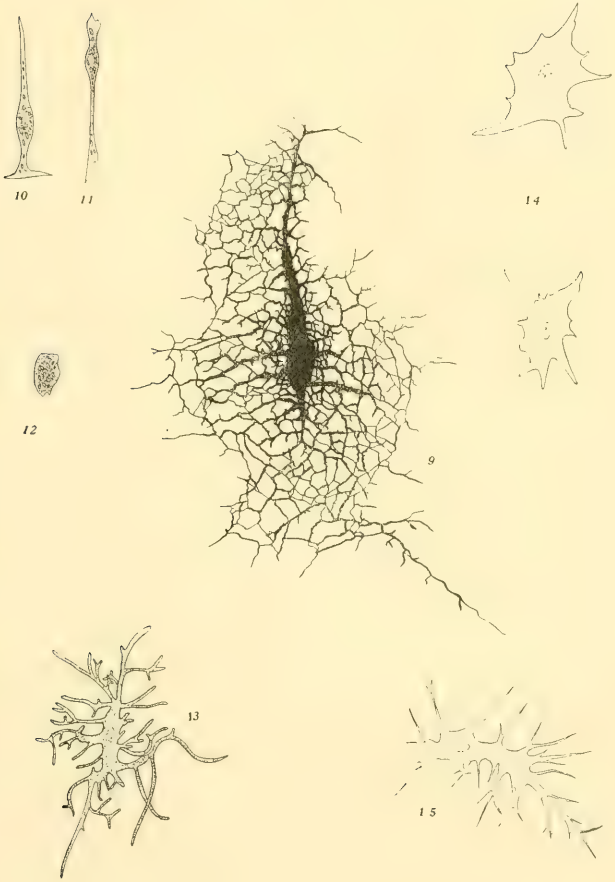
PLATE 6

Figs. 10, 11 and 12. Early stage in the development of a yellow pigment cell from the larva of *Hyla*. A few minutes after figure 10 was sketched the cell had assumed the form shown in figure 11. Figure 12 shows the contracted state assumed after the application of heat.

Fig. 13. A yellow pigment cell from a larva of *Diemyctylus*.

Fig. 14. Two leucophores from the ventral side of a young larva of *Diemyctylus*.

Fig. 15. Connective tissue cell from the tail of a larva of *Diemyctylus*. The cells shown in figs. 9, 13, 14 and 15 were not isolated from the surrounding tissues.


10
11
14
12
9
13
15

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY

Vol. 11, No. 8, pp. 155-172, pls. 7-8 September 24, 1913

BEHAVIOR OF ECTODERMIC EPITHELIUM OF TADPOLES WHEN CULTIVATED IN PLASMA

BY

S. J. HOLMES

The movement of epithelial cells in embryonic development, in regeneration and in various pathological processes has long been recognized; and an extensive literature has grown up in relation to various phases of the subject. But while the fact of such movement has been generally regarded as established, there has been considerable diversity of opinion as to the precise method by which epithelial cells change their position and as to the causes of their migrations. The formation of continuous epithelial membranes is to a large degree a matter of the behavior of the component cells. These cells have a marked tendency to arrange themselves in layers, and to fit closely together so as to leave no open spaces between them. The role of the latter tendency in relation to various osmotic processes in the organism is obvious. And we find that it is manifested as a rule by the cells of early embryonic development.

The blastula and gastrula in typical cases are composed of cells forming a perfectly continuous layer enclosing a cavity which contains fluid of a different osmotic pressure from that of the surrounding medium, a condition that could not be maintained in the absence of a continuous membrane. Even in early cleavage this tendency of the cells to fit together (the Cytarme of Roux) is very manifest. Later the same trait manifests itself in the formation of the germ layers, and the maintenance of the

layered arrangement, through the various foldings, invaginations and outpushings that play so prominent a part in the formation of organs in more advanced stages of development. While the direction of cell division, and His's principle of unequal growth are factors which may be influential in the production of these layered structures, it is evident that the appropriate behavior of the component cells is a factor of essential importance; and in certain cases at least it can be shown that, in the absence of cell division and any notable amount of growth, the behavior of the cells alone may lend to the formation of a membrane-like layer. The formation of epithelial layers is a factor of such general occurrence in embryonic processes that any study of the behavior of epithelial cells that will throw light upon the mechanism of this formation cannot fail to be of importance from the standpoint of causal morphology.

While the extension of epithelial layers over abraded surfaces or other solid substances has often been spoken of as if it were the result of cell multiplication or the passive shoving along of cells as a consequence of pressure, many studies have made it evident that the epithelial cells play an active rather than a passive role in this process. Active wandering of epithelial cells has been described in different animals as due to a sort of amoeboid movement more or less like that which occurs in leucocytes or certain cells of the mesenchyme. In a recent extended paper on the subject, however, Oppel has come to the conclusion that while the movement of epithelium depends upon the activities of the cells themselves it is not an amoeboid motion.

The experiments of Oppel (1912b) were performed on various kinds of epithelium from the dog, cat and rabbit. Small pieces of different organs were freed from epithelium over a part of their surface by scraping off the cells with a sharp scalpel. The pieces of tissue were then placed in blood plasma, incubated in a warm oven, and the progress of overgrowth of the denuded surface was followed partly by direct observation of the living tissue, but mainly by means of sections cut at different intervals of time after the preparations were made. Soon after the tissues were placed in plasma the epithelial cells near the cut surface began to extend upon the denuded connective tissue substratum, often

spreading out into a layer but one cell thick. Mitoses did not appear until a considerable amount of spreading had been accomplished. Although the outwandering cells commonly became more or less flattened, measurements showed that they did not increase appreciably in the extent of their surface. Movement occurred as a rule without pseudopods; nevertheless the cells changed considerably in form. No evidence could be found that the movements were determined by cellular contractility. Oppel compared the cells to partly filled sacks of inelastic material which could change their outline without varying the extent of their surface. The form changes are presumably correlated with the movements of the cells, and these movements, while made in response to external stimuli, are attributed to internal factors; but the real *modus operandi* of epithelial movement Oppel fails to make clear. Epithelial movement, which Oppel makes a distinct category of activity, has, according to him, the following characteristics:

"Die Epithelbewegung vollzieht sich nicht unter Aussenden von schmäleren oder breiteren Fortsätzen (sog. Pseudopodien), wie dies bei der Leucocytenbewegung der Fall ist."

"Die Epithelbewegung geht nicht mit Isolierung (absolute Selbständigkeit) der einfach einzelnen Zellen einher, sondern sie führt im Gegenteil zu einer flächenhaften Berührung gleichartiger Zellen (Cytarme).

"Die Epithelbewegung ist oft eine Massenbewegung. Ganze Zellgruppen bewegen sich miteinander infolge von Reizwirkung, jedoch mit steter Lageveränderung der einzelnen Zellen untereinander."

"Die zur typischen Gestaltung führende Epithelbewegung bleibt im wesentlichen auf die Oberfläche bindgewebiger Flächen beschränkt (Desmophilie)."

Lewis and Lewis (1912) have recently described membrane formation in the tissue of the chick embryos cultivated in various artificial media. These membrane-like outgrowths often spread out for a considerable distance into the surrounding medium. The cells at the edges of the outgrowth in many cultures were irregular in outline and sometimes ended "in long irregular processes with an enlarged fimbriated end". Many of the cells

became extremely flattened against the cover glass so there can be little doubt that the extent of their free surface was greatly increased; and the form of the free cells as well as those on the margins of the membranous outgrowths gave every appearance of amoeboid activity.

Since the tissues used in the cultures contained different kinds of cells it is not certain that the cells that formed the membranes were of epithelial origin. Wandering cells probably derived from connective tissue are exceedingly common in cultures of tissues *in vitro*, and while in several cases the membranes that were formed strikingly resembled the common forms of pavement epithelium, it is possible that they may have been of mesenchymatic origin.

In Harrison's paper (1910) on the development of nerve fibers from the neuroblasts of the frog embryo there is described the outgrowth of sheets of ectoderm in hanging drops of lymph. "Along the free border of these sheets of cells there often appears a fringe of hyaline protoplasm, which undergoes continuous amoeboid changes (figs. 13 and 14 pl. fr.). In one case of this kind it was observed that the sheet of cells gradually spread out toward the side on which the fringe was placed. Since the work of Peters ('85–'89) it has generally been admitted that wound healing in the epidermis is primarily due to the movement, in part amoeboid, of the epithelial cells, so that it seems quite possible that in this fringe of hyaline protoplasm above described, we have one part of the mechanism by which the movement of cells in wound healing is brought about". Observations to be described later bear out this conclusion.

My own experiments on the behavior of epithelial cells were made upon the embryos and young tadpoles of *Rana, Hyla* and *Diemyctylus*. It is more advantageous to work with the young tadpoles before they have made their escape from the jelly, as it is easier to obtain preparations free from infection. Treatment of the free tadpoles with antiseptics is liable to injure the epithelial cells and to diminish the vitality of the tissues if carried far enough to be effective. However, many successful preparations were made from older tadpoles. Bacteria develop more rapidly in fluid media such as serum, Ringer's, or Locke's solution than

in the coagulated plasma, partly perhaps because their spreading is less impeded, but also, I suspect, because the tissues thrive better in plasma and therefore have an antagonistic influence on the development of these organisms. It was often noticed that, while bacteria may be present in preparations of thriving cells, they often did not make much headway as long as the tissues were active.

As a rule the young embryos or tadpoles were cut into small pieces in sterile Ringer's solution. Both blood plasma and lymph were used as culture media. The latter is much more convenient to work with, as a drop of lymph can be easily transferred without coagulation by a sterile paraffin-coated pipette from a lymph sac of the adult to a cover slip. The piece of tissue was then placed in a drop of lymph and the cover slip sealed by pure vaseline over the cavity of a hollow ground slide. The lymph was often centrifuged to free it from corpuscles, but for the purpose of many experiments this operation was not necessary. No noticeable advantage resulted from using plasma diluted with distilled water, which was found by Carrel to be so valuable a medium for mammalian tissue. Both Ringer's and Locke's solutions were used as culture media, but while cells remained alive and active in these fluids for several days, and even weeks, they were not found nearly so suitable as lymph and plasma, or even serum. As a rule each culture was made in blood plasma or lymph of its own species. Cells of the tadpoles of *Hyla, Rana,* and *Diemyctylus* would live and manifest some activity in the lymph or plasma of other amphibians, but they did not thrive so well as in fluids from members of the species to which they themselves belonged. The tissues in the earlier experiments were kept at ordinary room temperature, but later they were placed in an ice chest whose temperature varied from 8° to 15° C. where they thrived better and lived longer. Many preparations remained alive at ordinary temperature for over two months. At intervals of from a few days to a week the tissues were usually transferred to fresh lymph or plasma. Several preparations, however, were kept alive for over six weeks without change of medium. When the changes were made the pieces of tissue were washed for several minutes in Ringer's solution before being placed in fresh

lymph or plasma. The transfer in many cases was obviously beneficial, as tissues which were beginning to show signs of deterioration very frequently became more active and presented a more healthy appearance after being placed in the fresh medium. In many preparations the cover slips were raised and replaced every few days so as to allow a change of air in the cell, but it was not discovered that this procedure enabled the cells to thrive any better than in preparations that were not so treated.

Most of the preparations for the study of epithelium were taken from the tail of the young tadpole. The thin transparent expansion of this organ contains a relatively large amount of epithelium, the thin median portion consisting mainly of connective tissue with branching cells embedded in a comparatively firm matrix. The connective tissue elements of such preparations remained relatively fixed in position, the movements of cells being confined mainly to the ectoderm. The ectodermic cells, especially in the older tadpoles, are so easily distinguished by their structure and diffuse granular pigmentation that their recognition does not present the least difficulty.

Within twenty-four hours after the pieces were mounted, strands of epithelium were to be seen in many cultures extending into the plasma. Around the piece there were also a number of free epithelial cells which had become loosened from their attachment and had wandered out into the fluid. In preparations several days old these free cells were more numerous and scattered over a wider area. Epithelial cells from young embryos with but a short stub of a tail are relatively less active than those from older larvae. The reason for this is probably that they are crowded so full of yolk granules that changes of form are considerably impeded. Epithelial cells from the ventral side of young embryos are less active than those from the dorsal side, doubtless because they have more yolk and less protoplasm. Nevertheless the thin protoplasmic outer part of these cells shows active amoeboid movements, putting out fine processes here and drawing them in there, and it is very probably on account of such movements that the cells are able to slowly change their position. In older larvae the yolk in the ectodermal cells gradually disappears and the relative proportion of protoplasm greatly

increases, although small yolk granules may be seen in the cells of the free swimming tadpoles. Parallel changes in the yolk content of cells occurred in pieces of tadpole tails kept several weeks in lymph. Many preparations in which the ectoderm cells were crowded with yolk globules when first put up had assimilated most of the yolk and became nearly transparent after being kept for two or three weeks *in vitro*. Some pieces, as will be more fully described in another paper, underwent a considerable increase in volume. The ectoderm had extended over the cut surface so as to form a perfectly continuous investment and the cells had become thinned out and widened to two or three times their original diameter, while the original yolk content had been almost entirely used up, leaving the cells nearly transparent.

With the disappearance of the yolk the ectodermal cells are rendered capable of spreading out more widely. Those that become free usually remain more or less rounded in outline unless they come into contact with a solid surface. The older ectoderm cells then manifest an extraordinary capacity for spreading. The area in contact with the substratum becomes increased by the emission of short fine and very transparent pseudopods. By this means the cells are enabled to extend in all directions at the same time. The margins of these cells are usually irregular, and one may usually observe changes in their outlines and follow various stages in the spreading of the cytoplasm. Cells frequently spread out on the cover slip so as to become of extreme thinness. Except for a small granular area around the nucleus the cytoplasm may be so very transparent that it is invisible under ordinary conditions, and the true extent of the cell can be ascertained only by observing its delicate amoeboid boundary. Neighboring cells as a consequence of this spreading frequently come into contact, and where there are several of them near together they may form a continuous membrane. In plate 7, figure 5, is shown a small part of a secondary membrane formed in this way. The cells composing it had originally become scattered through the plasma; then they began to flatten out, the process continuing until no open spaces remained between the cells. In this case the secondary membrane so formed

covered the larger part of the surface of the cover glass in contact with the hanging drop of plasma. The boundaries of the cells were mostly hexagonal and the appearance of the membrane was very much like of the shed cuticle of the adult amphibian.

Membranes like the one just described are called secondary because by following the method of their formation it was found that they were the result of the fusion of originally separate cells. Many other similar membranes were observed to arise from the implanted issue by the outgrowth of a continuous sheet of ectoderm. The thickness of these outgrowths varied from one to three or four cells deep. Generally they were thinner towards the periphery, and the outermost cells usually presented a thinned out and finely amoeboid margin.

In many cases the ectodermic epithelium was drawn out into very long strands. These usually became manifest in two or three hours after the preparation was made, but they reached their maximum extension as a rule in three or four days. Frequently the length of the strands was several times the diameter of the piece from which they originated, and they were usually several cells in thickness, but occasionally were reduced to a single row of overlapping cells. The cells were generally fusiform with the long axis parallel to the strand. As a rule these strands were in contact with the cover slip, but they frequently crept out upon the surface of a coagulated portion of the surrounding medium. In several preparations fibers of cotton wool were introduced, and where the epithelial cells came in contact with the fibers they crept out upon them to a considerable distance. It is common to find the fibers completely surrounded by an investment of epithelium. The extension of epithelium always occurred at some break in the surface. In figure 1 is shown a piece of a cross section of the tail of a *Hyla* tadpole taken near the tip. The epithelium had covered the posterior cut surface, and at the meeting point of the approaching edges of the extending sheets of cells a long strand had grown out posteriorly, reaching on the third day the extent illustrated in the figure.

In a section of the tail of tadpole of *Rana* (pl. 7, fig. 2) there is shown a similar posterior extension of ectoderm, but in addition there are strands proceeding from the anterior edge of the

piece. The posterior curve of these strands is due to the fact that they are extending along surfaces of coagulated plasma. The small amount of Ringer's solution that was introduced as the tissue was transferred to the culture medium caused the area around the tissue to remain fluid, while the surrounding plasma was coagulated. As the posterior extension of epithelium reached the coagulated plasma it began to extend along its surface in both directions. The outer boundaries of the cellular extensions, if continued, would describe a nearly circular fluid area within the coagulated material. Subsequently the thin middle part of the posterior extension was pulled apart, resulting in the formation of an independent island of cells which gradually became more compact, while the part attached to the old piece was drawn in.

The section of the tail of *Rana* (pl. 7, fig. 3) developed only a slight posterior extension of cells, but from the cut ends of the ectoderm of one side long strands grew out laterally and finally met and fused. After the fusion the strands began to spread out on either side upon the cover slip. While the cells of the narrow part of the strand were fusiform those of the extensions were hexagonal and much flattened. The margins of these extensions were thin and hyaline and showed the fine amoeboid processes previously described. While this preparation was being studied under the microscope the thin strand shown in the lower part of the figures was seen slowly to contract owing possibly to the higher temperature to which it was exposed during observation. As it shortened it could be seen to become thicker and the individual cells became less elongated. The next day, the fourth after the preparation was made, this strand had become considerably shorter, the extension of cells from the opposite strand had become wider and the enclosed space between the strands reduced to less than a fourth the size shown in the figure.

In a remarkable extension from the tail of the tadpole of *Rana* (pl. 7, fig. 4) the cells grew out along a fiber of cotton, t', which lay under the piece, and was covered over by the proximal part of the strand so that its middle portion is not seen. Where another cotton fiber, t, crossed the first the strand of cells left

the latter and crept along the second fiber. At the same time a second strand of cells branched off from the first, and pursued its course independently of the two fibers and about midway between them.

After several days the strands in all the preparations showed a tendency to draw in and form more compact masses. Often they were drawn back to the original piece, forming a large clump of cells which persisted with little change of form, though remaining alive for weeks. Sometimes the larger strands would break up into separate masses of cells which would aggregate into more or less rounded masses. Gradually the activity of the epithelial cells, even when frequently changed to fresh media, became more and more reduced, although in some cases they presented a normal appearance for over two months.

The striking behavior of these extensions of the ectoderm naturally raises several questions as to the nature and causes of movements involved. Are the strands and sheets of cells pushed out or pulled out? Are they due to growth or cellular activity? Do the cells increase in number after implantation in plasma? What part, if any, do tropic responses play in producing the observed results? In regard to the first question some observations made on the preparation shown in figure 4 are significant. At the time the culture had assumed the form shown in the figure especial attention was bestowed upon the tip of the narrow strand that lay between the two fibers of cotton. The changes witnessed during the few hours that the part was kept under observation are illustrated in figures 8–11. The tip could be seen to be very slowly advancing, and many of the cells showed a broad, thin hyaline border which was furnished with fine pseudopods and irregular lobes of protoplasm. These were especially well developed at the extreme tip of the process and on a small lobe a short distance behind the tip; elsewhere this whole branch was devoid of pseudopods and the cells presented no clear expansions. The hyaline extensions of protoplasm were the seat of amoeboid activity; the changes in the small lobe mentioned are shown in figure 8, *a*, *b*, *c*. A mark of an eye-piece micrometer (shown by a dotted line) turned so as to lie across the tip of the extension made it possible to follow a very

slow advance of the cells. After the strand had advanced about twice the diameter of the terminal part of the extension the tip apparently lost its grip upon the cover glass and was suddenly pulled back so as to lie entirely behind the mark. At the same time it became turned somewhat toward one side (pl. 8, fig. 9). Soon the terminal portion began to advance again, the kink between it and the rest of the strand became straightened out, the part immediately behind the clear extremity became longer and narrower as if it were being pulled out (figs. 10, 11). The lateral lobe near the tip gradually became less prominent, its hyaline border narrow and the pseudopods smaller. Finally with the further extension of the tip, to which it was apparently acting more or less in opposition, it was drawn in entirely.

The behavior of the hyaline tip of the strand whose pseudopods acted much like those of an advancing rhizopod, the straightening out of the bend, and the form changes of the region behind the tip, indicate that the strand was pulled out by the amoeboid activity of the terminal protoplasm, rather than pushed out from behind. And the fact that the tip of the strand was suddenly pulled backward indicates that its advance was effected against a certain tension of the proximal part of the stand.

Actual growth of cells probably plays but a small part in the production of the extensions described. The cells composing them are no larger than in places where there is practically no change; and the structures are produced too rapidly for either the growth or the multiplication of cells to be factors of prime importance.

The ectoderm cells possess to a remarkable degree the property of thigmotaxis which is so prominent a trait of amoeboid protozoans. Apparently they are indifferent as to the kind of solid object to which they attach themselves, since they readily extend upon the surface of glass, cotton fiber, clots of plasma as well as their normal substratum of connective tissue. They also readily extend upon one another, exercising a sort of mutual attraction which tends to keep them in continuous masses. They are also very free to move past one another and to shift about their relative positions. Those protoplasmic strands or bridges which may have joined them together in their normal situations

are unable to check their "Wanderlust" when an opportunity presents itself for migrating over a greater extent of surface. The individual cells, as we have seen, manifest a tendency to spread out so as to bring as large a part of their surface as possible in contact with the substratum. And it seems very probable that the extension of strands and sheets of ectoderm is brought about by the same kind of activity that occasions the spreading of the individual cells. The method by which the ectodermic epithelium of tadpoles comes to spread out over surfaces is probably different, therefore, from that which Oppel concludes is followed by the epithelial cells of mammals.

When conditions become unfavorable the cells tend to assume a more rounded form. This tendency is probably responsible for the shortening and thickening of strands that were several times observed, and the drawing in of cords of cells. I have been able to cause a contraction of strands of cells by touching the cover glass above them with a warm needle. The same treatment causes the individual cells to draw in their pseudopods. Not only do epithelial cells respond in this manner to thermal stimuli, but in the more irregular cells of the mesenchyme the response is more decided. In pigment cells the retraction of the processes, while evident, is less pronounced. A sharply defined band of strong light focused on the epithelial cells had very little effect upon their activity.

Several experiments were undertaken in order to ascertain if the epithelial cells in the cultures actually increased in number. Small pieces of tissue were placed in serum, and after a number of cells had become free from the piece, a small part of the serum was drawn into a very fine pipette and transferred to a larger drop of the same substance which was sealed up in the usual manner. In this way a small number of cells were usually transferred and these were carefully counted and recorded. They were then recounted at intervals of one or more days. In several cases a part of the cells was transferred after two or three days to fresh serum or plasma, and counted at different times for some weeks. In many of the preparations it was found that in the first two days the number of cells had considerably increased; in a few instances it had doubled; and a second

count showed a further increase on the third day, but after four or five days the increase in number was very small. Transferring the cells to fresh media failed to cause more than a very slight increase in number. The possibility suggested itself that by taking cells from young embryos and transferring them at intervals into fresh media a continuous culture might be carried on for some time. Whether through inadequate technique or for some other reason this hope was not realized, despite many careful experiments. In many preparations the cells remained to all appearances healthy for three months. In the cells from comparatively young embryos there was little evidence of progressive change. The yolk content remained apparently the same in these cells for over two months, and the cells showed but little activity, although they were quite normal in appearance. Beyond making one or two divisions the isolated ectoderm cells from young embryos failed to undergo any well-marked developmental changes.

Older ectoderm cells which had used up most of their yolk were more active, showing marked changes in form and especially flattening out upon solid surfaces. The older cells that were isolated and counted failed to give more than a slight increase in number. The cilia in many cases kept beating for several weeks. Some of the cells that had become greatly flattened out showed in a few cultures various stages of amitotic division of the nucleus. In different cells the nucleus was constricted from a slight indentation to an almost complete division, and several cells were found which contained two clearly separate nuclei. No convincing evidence could be obtained, however, that the amitotic division of the nucleus was followed by a division of the cytoplasm.

Harrison (1912) has observed the differentiation of isolated cells from frog embryos, and I have been able in several cases to confirm his findings. But, so far as my rather limited experience goes, isolated single embryonic cells especially of the ectoderm, do not differentiate nearly so well as those forming a part of an organized piece of tissue. Several times I have observed pieces of embryos increase in size, become more transparent, and show transformations of the internal parts; and along with

these changes the cells of the ectoderm would gradually use up their yolk and undergo modifications closely similar to those followed in normal development. In the same cultures isolated ectodermic elements were usually present, but they remained, except for some changes of form, nearly the same as when first mounted. The masses of cells that remained, so to speak, out of the organization failed for some reason to keep pace with the cells from which they had been separated. So far as conditions for nutrition, respiration and excretion were concerned, the advantages would seem to be with the isolated cells. Their failure to differentiate so well as the others may be due to the absence of certain conditions of stimulation that are supplied by their normal association with other cells, rather than the untoward influences of the surrounding medium. What these conditions are is at present obscure. Whether tissue culture will make it possible to apply methods of analysis which will disentangle any of them remains to be seen.

SUMMARY

1. Pieces of the body of late embryos or young tadpoles of various amphibians cultivated in lymph or plasma frequently send out extensive strands or sheets of ectodermic cells into the surrounding medium.

2. The cell masses tend to extend upon some solid surface such as the cover slip, fibers of cotton, or the surface of a coagulated mass of plasma.

3. The isolated cells of ectodermic epithelium show a tendency to spread out widely and to creep along a solid surface. Scattered cells which come into contact in the course of their spreading may form a perfectly continuous secondary membrane.

4. Active epithelial cells have a thin clear margin of protoplasm which puts forth fine pseudopods and undergoes marked changes in outline. It is probably by means of this amoeboid movement that the spreading and migration of individual cells are accomplished.

5. Evidence from several facts was obtained to show that the masses of cell that were put forth were not pushed out, and did not grow out, but were drawn out by the amoeboid activity of the cells at the free surface of the mass.

6. Unfavorable conditions tend to make the epithelial cells assume a rounded form. Heat causes them to retract their pseudopods and makes the strands of cells contract and break up into masses.

7. There is a limited amount of multiplication in the isolated cells of the ectoderm.

8. Amitotic divisions of the nucleus may occur *in vitro*, but they were not found to be followed by a cleavage of the cytoplasm.

9. Isolated cells from young embryos undergo comparatively little differentiation, while cells that form a part of an organized mass of tissue may continue to develop.

BIBLIOGRAPHY

Barfurth, D.

1891. Zur Regeneration der Gewebe. Arch. mikr. Anat., **37**, 406–491, pl. 22.

Eycleshymer, A. C.

1907. The closing of wounds in the larval *Necturus*. Am. Journ. Anat., **7**, 317–325, 10 figs. in text.

Fraisse, P.

1885. Die Regeneration von Geweben und Organen bei den Wirbeltieren (T. Fischer, Cassel und Berlin), viii + 164, 3 pls.

Harrison, R. G.

1910. The outgrowth of the nerve fiber as a mode of protoplasmic movement. Jour. Exp. Zool., **9**, 787–848, pls. 1–3.

1912. The cultivation of tissues in extraneous media as a method of morphogenic study. Anat. Rec., **6**, 181–193.

Lewis, M. R. and Lewis, W. H.

1912. Membrane formations from tissues transplanted into artificial media. Anat. Rec., **6**, 195–205, 4 pls.

Loeb, L.

1902a. Ueber das Wachstum des Epithels. Arch. f. Ent.-mech., **13**, 487–506, pl. 20.

1902b. On the growth of epithelium in agar and blood serum in the living body. Jour. Med. Res., **8**, 109–115, pls. 9–11.

Oppel, A.

1912a. Causal-morphologische Studien. IV Mitteilung. Arch. f. Ent.-mech., **34**, 133–167, pls. 9, 10.

1912b. *Idem*. V, Mitteilung, *Ibid.*, **35**, 371–456, pl. 8.

Peters, A.

1885. Ueber die Regeneration des Epithels der Cornea. Inaug. Diss. Bonn.

1889. Ueber die Regeneration des Epithels der Cornea. Arch. mikr. Anat., **33**, 153–162.

EXPLANATION OF PLATES

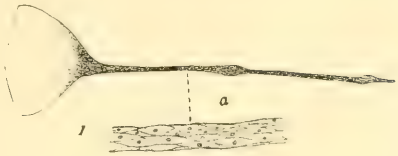
PLATE 7

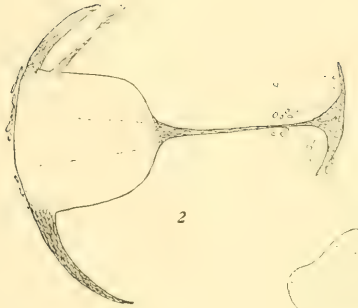
Fig. 1. Extension of ectoderm from a section near the tip of the tail of a *Hyla* tadpole. The extension of cells, shown more highly magnified in *a*, proceeds from the middle of the posterior cut surface.

Fig. 2. Section across the tail of a tadpole of *Rana* showing a strand of ectoderm extending from the middle of the posterior end, and other strands at the anterior end extending along the surface of the coagulated plasma.

Fig. 3. Lateral extensions of cells from a section of the tail of a tadpole of *Rana*. The strands in places have widened into sheets of cells.

Fig. 4. Strands of cells from a tadpole of *Rana* extending along and between fibers of cotton.


a
1


2

3

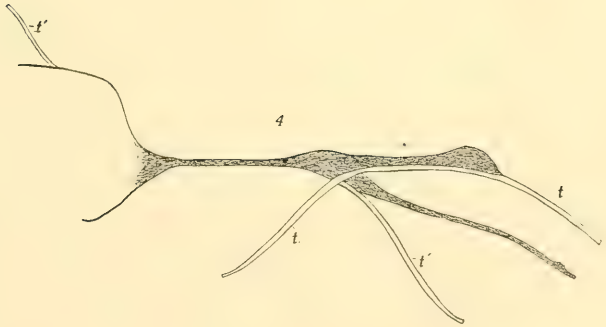

t'
4
t
t
t'

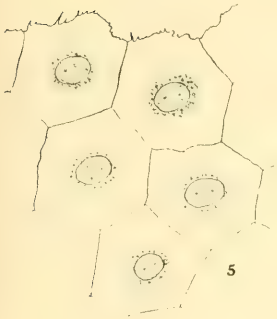
PLATE 8

Fig. 5. A secondary membrane formed by the approximation of originally separated cells from the ectoderm of a tadpole of *Hyla*.

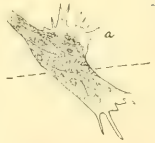
Figs. 6, 7. Isolated ectodermic cells from the same preparation from which figure 5 is taken. In 6 there is a long cytoplasmic process ending in a clear amoeboid expansion.

Fig. 8. Tip of the process shown in figure 4 that extends between the two fibers of cotton; *a*, *b*, *c* represent successive changes in the hyaline border of the lobe *a*.

Figs. 9–11. Stages in the extension and form changes of the tip of the process shown in figure 8. The dotted lines indicate a mark on the micrometer set to gauge the progress of the strand of cells.

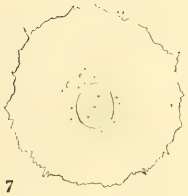


5

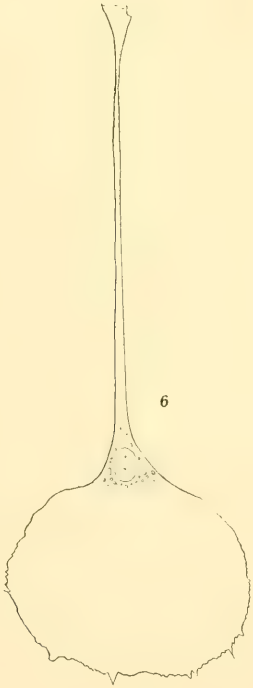


8

9

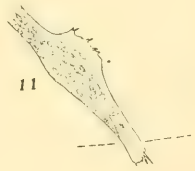


7



6

10



11

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY
Vol. 11, No. 9, pp. 173-180, pl. 9 November 26, 1913

ON SOME CALIFORNIAN SCHIZOPODA

BY
H. J. HANSEN

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY

Note.—The University of California Publications are offered in exchange for the publications of learned societies and institutions, universities and libraries. Complete lists of all the publications of the University will be sent upon request. For sample copies, lists of publications or other information, address the Manager of the University Press, Berkeley, California, U. S. A. All matter sent in exchange should be addressed to The Exchange Department, University Library, Berkeley, California, U. S. A.

OTTO HARRASSOWITZ, LEIPZIG.

Agent for the series in American Archaeology and Ethnology, Classical Philology, Education, Modern Philology, Philosophy, Psychology, History.

R. FRIEDLAENDER & SOHN, BERLIN.

Agent for the series in American Archaeology and Ethnology, Botany, Geology, Geography, Mathematics, Pathology, Physiology, Zoology, and Memoirs.

ZOOLOGY.—W. E. Ritter and C. A. Kofoid, Editors. Price per volume, $3.50. Commencing with Volume II, this series contains Contributions from the Laboratory of the Marine Biological Association of San Diego.

Cited as Univ. Calif. Publ. Zool.

Volume 1, 1902-1905, 317 pages, with 28 plates $3.50

Volume 2 (Contributions from the Laboratory of the Marine Biological Association of San Diego), 1901-1906, xvii + 382 pages, with 19 plates $3.50

Volume 3, 1906-1907, 383 pages, with 23 plates $3.50

Volume 4, 1907-1908, 400 pages, with 24 plates $3.50

Volume 5, 1908-1910, 440 pages, with 34 plates $3.50

Vol. 6.

1. (XXIII) On the Weight of Developing Eggs. Part I, The Possible Significance of Such Investigations, by William E. Ritter; Part II, Practicability of the Determinations, by Samuel E. Bailey. Pp. 1-10. October, 1908 ..... .10
2. (XXIV) The Leptomedusae of the San Diego Region, by Harry Beal Torrey. Pp. 11-31, with 11 text-figures. February, 1909 ..... .20
3. (XXV) The Ophiurans of the San Diego Region, by J. F. McClendon. Pp. 33-64, plates 1-6. July, 1909 ..... .30
4. (XXVI) *Halocynthia johnsoni* n. sp.: A comprehensive inquiry as to the extent of law and order that prevails in a single animal species, by Wm. E. Ritter. Pp. 65-114, plates 7-14. November, 1909 ..... .50
5. (XXVII) Three Species of *Cerianthus* from Southern California, by H. B. Torrey and F. L. Kleeberger. Pp. 115-125, 4 text-figures. December, 1909 ..... .10
6. The Life History of *Trypanosoma dimorphon* Dutton & Todd, by Edward Hindle. Pp. 127-144, plates 15-17, 1 text-figure. December, 1909 ..... .50
7. (XXVIII) A Quantitative Study of the Development of the Salpa Chain in *Salpa fusiformis-runcinata*, by Myrtle Elizabeth Johnson. Pp. 145-176. March, 1910 ..... .35
8. A Revision of the Genus *Ceratocorys*, Based on Skeletal Morphology, by Charles Atwood Kofoid. Pp. 177-187. May, 1910 ..... .10
9. (XXIX) Preliminary Report on the Hydrographic Work Carried on by the Marine Biological Station of San Diego, by George F. McEwen. Pp. 189-204; text-figure and map. May, 1910 ..... .15
10. (XXX) Biological Studies on *Corymorpha*. III, Regeneration of Hydranth and Holdfast, by Harry Beal Torrey. Pp. 205-221; 16 text-figures.
11. (XXXI) Note on Geotropism in *Corymorpha*, by Harry Beal Torrey. Pp. 223-224; 1 text-figure.

    Nos 10 and 11 in one cover. August, 1910 ..... .20
12. The Cyclostomatous Bryozoa of the West Coast of North America, by Alice Robertson. Pp. 225-284; plates 18-25. December. 1910 ..... .60
13. Significance of White Markings in Birds of the Order Passeriformes, by Henry Chester Tracy. Pp. 285-312. December, 1910 ..... .25
14. (XXXIII) Third Report on the Copepoda of the San Diego Region, by Calvin Olin Esterly. Pp. 313-352; plates 26-32. February, 1911 ..... .40
15. The Genus *Gyrocotyle*, and Its Significance for Problems of Cestode Structure and Phylogeny, by Edna Earl Watson. Pp. 353-468; plates 33-48. June, 1911 ..... 1.00

Index, pp. 469-478.

* Roman numbers indicate sequence of the Contributions from the Laboratory of the Marine Biological Association of San Diego.

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY

Vol. 11, No. 9, pp. 173-180, pl. 9 November 26, 1913

ON SOME CALIFORNIAN SCHIZOPODA

BY
H. J. HANSEN

In his valuable work, "Synopsis of California Stalk-eyed Crustacea," Holmes (1900) established or redescribed a number of Schizopoda, among which were two species of the genus *Thysanoessa*. When I began to write a preliminary account of all the genera and species hitherto captured of the Euphausiacea I applied to the University of California, asking for the loan of the material in their collections of the Euphausiacea, together with specimens of some of the species of Mysidacea established by Holmes (1900). Dr. C. A. Kofoid most benevolently sent me what he could. I obtained specimens of the two species of *Thysanoessa* described by Holmes (1900), some material taken in stomachs of the salmon, and specimens of some of Professor Holmes's Mysidacea. The specimens from salmon stomachs were taken in Alaska, and were collected by Mr. F. M. Chamberlain of the United States Bureau of Fisheries. Permission to use this material has kindly been granted by Dr. H. M. Smith, United States Commissioner of Fish and Fisheries.

On the following pages I list the species of the collection and I redescribe to a certain degree three of them. The descriptions of Holmes are on the whole good as far as they go, but in later years I have seen so many species of the genera in question that I find it necessary to point out some features of special importance for the recognition and classification of these species from California.

I. Euphausiacea

As to literature, it may be sufficient to refer to my paper (1911), "The Genera and Species of the Order Euphausiacea."

1. **Euphausia pacifica** H. J. H.

Euphausia pacifica H. J. Hansen (1911), p. 28, fig. 10

A number of moderately preserved specimens from stomachs of ten dog-salmon *Onchorhynchus keta* (Walbaum), Admiralty Head, Whitby Island, Alaska, June 30, 1903.

2. **Thysanoessa spinifera** Holmes

Thysanoessa spinifera H. J. Hansen (1911), pp. 38, 41

Holmes (1900) has published a good description with figure of his single specimen. In the paper quoted (1911) I have added some particulars, basing them on material from the United States national Museum, and in a future paper a new representation of this fine species will be given.

A couple of small specimens, of which at least the larger belongs probably to *T. spinifera*, were taken from seven dog-salmon (*Onchorhynchus keta*) fingerlings, Dundas Bay, Alaska, July 24, 1903.

3. **Thysanoessa raschii** M. Sars

Thysanoessa raschii, H. J. Hansen (1911), pp. 38, 42

Three specimens, but unfortunately without locality, taken in stomachs of salmon belong to this species. A single specimen was found among the above named specimens of *Euphausia pacifica* from dog-salmon, taken at Admiralty Head, Whitby Island, June 30, 1903. Fragments from dog-salmon stomach, Isanotski Straits, Alaska, July 15, 1904, seem to belong to this species.

4. **Thysanoessa gregaria** G. O. Sars

Thysanoessa gregaria H. J. Hansen (1911), pp. 39, 43–44, fig. 15

Having examined three specimens named by Holmes, I can confirm his determination. It is interesting that this species has also been taken off California, at Avalon, Santa Catalina Island.

II. Mysidacea

1. **Siriella pacifica** Holmes

Pl. 9, figs. 1*a-f*

In the report on the "Siboga" Schizopoda I (1910) enumerated twenty species of this genus, eleven of which were established as new to science, and some hitherto overlooked or not sufficiently valued characters were pointed out. As to *Siriella pacifica* Holmes, I stated that it "ought to be re-examined," because it probably belongs "to a group of the genus, whose forms must be established on full-grown males, as the females in two or three cases cannot be separated with certainty, while the males show excellent specific characters in the fourth pair of pleopods."

Having now examined two specimens determined by Holmes, viz., an adult male and a female, my supposition as to the affinities of *S. pacifica* prove to be correct. The species is on the whole more nearly related to *S. inornata* H. J. H. and *S. media* H. J. H. than to any other form.

Description.—Moderately robust. Carapace in both sexes somewhat produced, the frontal plate (pl. 9, figs. 1*a*, 1*f*) being a broad, rather low triangle with the vertex somewhat produced, acuminate and acute. Eyes in the male (fig. 1*a*) considerably smaller than in allied forms, seen from above conspicuously shorter and narrower than the last joint of the peduncle, the posterior margin of which is rather convex; eyes in the female distinctly larger than in the male, seen from above (fig. 1*f*) conspicuously shorter but slightly broader than the peduncular joint. Antennule in the male with third peduncular joint only a little longer than broad; flagellum in the male extremely long, reaching beyond the hind margin of fourth abdominal segment. Antennal squama subequal in both sexes, with the terminal lobe much broader than long (fig. 1*a*).

Pseudobranchial rami on second to fourth pairs of male pleopods somewhat circularly curved, less spirally twisted than in *S. inornata*. Both rami of third pair of male pleopods terminating in a robust, spiniform, nearly straight, seemingly naked seta not longer than the normal setae on the preceding joint and with the

end obtuse. Each ramus of fourth pair of pleopods with peculiar setae; the endopod (fig. 1*c*, *en*) terminates in two strong, naked, spiniform setae, the other seta almost straight, about as long as the sum of the three distal joints, the inner seta distinctly shorter and less thick than the outer and somewhat angularly bent before the middle; the exopod terminates in two setae (fig. 1*e*, *ex.*), one very short, while the other is nearly as long as the long seta on the endopod, naked, robust, and somewhat before the middle strongly bent in a very peculiar way. These setae are quite similar in both uropods of the fourth pair. Finally the inner angle of the penultimate joint has a nearly straight, naked, strong seta scarcely as long as the long terminal seta.

Uropods moderately slender (fig. 1*d*). The exopod overreaches conspicuously the endopod; its proximal joint is almost three times as long as the distal, with fourteen or fifteen spines occupying somewhat more than half of its outer margin; distal joint not fully twice as long as broad. Telson somewhat less than three times as long as broad, reaching a little beyond the articulation of the exopod; along a little more than the distal half each lateral margin has an arrangement of spines nearly as in *S. inornata*, as above nine or ten long spines are distributed so that proximally four or three shorter spines are found in each interval between two long spines, while distally three or two (or only one) are found in each interval (fig. 1*e*). The terminal margin of the telson has three somewhat small spines placed between the single pair of very long and strong spines.

Length of both sexes, 9 millimeters.

Remarks.—The male of *Siriella pacifica* differs from all other species of *Siriella* hitherto described, excepting *S. anomala*, by having distal setae on both third and fourth pairs of pleopods modified, but it differs abundantly from the last named species in having the setae modified not only on the endopods but also on the exopods of these pleopods, in the shape of the antennal squama of the exopod of the uropods, etc. The female may be separated from those of *S. inornata*, *S. media*, etc., by its somewhat smaller eyes.

2. **Mysis costata** Holmes

Pl. 9, figs. 2*a-d*

Of this curious form only a moderately preserved female specimen is at hand. Since Czerniavsky (1882–83) subdivided the genus *Mysis* (*sens.* Sars 1877 and 1879) into a number of genera, several allied genera have been established by various authors. It is easily to be seen that if most or nearly all of these genera shall be maintained, then *M. costata* cannot remain in the genus *Mysis* together with its type *M. oculata* O. Fabr.; furthermore, *M. costata* can scarcely be referred to any among the more recently established genera, but nevertheless I think it advisable not to erect a new genus for its reception before a more detailed account of the appendages can be given. *M. costata* is more nearly related to *Neomysis* Czern. than to any of the other genera. The labrum has a frontal process about as long as in *Neomysis vulgaris,* but in *M. costata* this process is very acute and much more slender than in *N. vulgaris.* The antennal squama has the end narrowly rounded with two or three terminal setae (fig. 2*a*). The transverse ridges, mentioned by Holmes (1900), on the first to the fifth abdominal segments (fig. 2*b*) are dorsal foldings of the skin, so formed that, when the animal is seen from the side, the dorsal line of these abdominal segments looks as if a good number of such segments were present with the front margin of each such "segment" covered by the hind margin of the preceding one; but these foldings do not reach the lateral margins of their segments, as of course is the case with the articulations between the real segments. The sixth segment (fig. 2*b*, VI) has the first transverse "ridge" produced into a median, free, triangular plate (Holmes naming it a spine is less correct); the posterior part of the dorsal surface of this segment is sculptured in a peculiar way, and the middle of the posterior margin is produced in a smaller, triangular plate.

The telson (figs. 2*c*-2*d*) has the proximal third of each lateral margin considerably more concave than in *Neomysis,* while its outline otherwise is more like that in the last named genus than in any other form of *Mysis sens. lat.* Each lateral margin has from the base to near the end fourteen or fifteen long spines;

from near the middle of each margin the spines increase conspicuously in length backwards, and the intervals are occupied by quite small spines, one or two in the first interval, four spines in most of the other intervals, while no small spines are found between the larger ones along the proximal half of the lateral margins. The telson is subtruncate with four terminal spines; those of the median pair are very large, while those of the outer pair are less than half as long.

Length of the specimen seen, 8 millimeters.

3. **Neomysis franciscorum** Holmes

Pl. 9, figs. 3*a*, *b*

The single mutilated type-specimen is at hand. Holmes (1900) said: "This species is closely allied to *Neomysis rayii* (Murdoch) from Point Barrow, but differs in having the telson acute instead of 'truncated', and in having the terminal portions of the thoracic legs divided into a greater number of articulations." Whether the last named feature is of real value as a specific character I am not prepared to decide, but Holmes's statement that the telson is acute in *N. franciscorum* is incorrect. In order to make *N. franciscorum* recognizable I have drawn two figures (pl. 9, figs. 3*a*, *b*). The species is very closely allied to *N. rayii* Murdoch, of which I have two co-types (received from the United States National Museum) and a large number from various localities in northeastern Asia.

The antennal squamae are long and very narrow in both species, but both squamae of *N. franciscorum* having lost the distal part no possible difference between the two species in this feature can be pointed out by me. The eyes and eye-stalks are subsimilar in both forms, perhaps comparatively a little more slender in *N. rayii*. The frontal plate of the carapace is in *N. franciscorum* (fig. 3*a*) considerably shorter than in *N. rayii;* in *N. franciscorum* it is considerably less than half as long as broad, while in *N. rayii* it is longer and proportionately narrower, being distinctly more than half as long as broad. The telson (fig. 3*b*) is proportionately narrower than in *N. vulgaris,* being somewhat more than two and a half times as long as broad, but otherwise, in the main, as in the last named species. Each margin has

twenty-four or twenty-five somewhat short spines, the more distal pairs decidedly longer than those on the proximal half; the end is truncate and had been furnished with a couple of spines lost in the specimen, and between these spines an extremely small pair of spines is discernible. In *N. rayii* the telson has only nineteen to twenty-one or twenty-two spines on each lateral margin, and its most distal part is distinctly broader than in *N. franciscorum*, the terminal part between the last pair of lateral spines and the end being in *N. rayii* broader than long, in *N. franciscorum* only as broad as long.

Judging from the conspicuous difference in the length of the frontal plate between *N. franciscorum* and *N. rayii*, together with the smaller differences in the number of lateral spines and the shape of the terminal part of telson, I am inclined to think that *N. franciscorum* is a valid species. Unfortunately only a single specimen has been seen.

Zoological Museum, Copenhagen, Denmark.

Transmitted September 8, 1913.

LITERATURE CITED

Czerniavsky, V.

1882–83. Monographia Mysidarum imprimio Imperii Rossici (marin., lacustr. et fluviatilium) Fasc. I. Arb. St. Petersburg Naturf. Ges., **12**, Beilage, 170 pp.; Fasc. II. *Ibid.*, **13**, 1–85, pls. 1–4; Fasc. III. *Ibid.*, **18**, i-viii, 1–102, pls. 5–33.

Hansen, H. J.

1910. The Schizopoda of the Siboga Expedition. Res. Siboga Exped., **37**, 123 pp., 16 pls.

1911. The genera and species of the order Euphausiacea, with an account of remarkable variation. Bull. Inst. Océanogr. Monaco, **211**, 54 pp. 18 figs. in text.

Holmes, S. J.

1900. Synopsis of California stalk-eyed Crustacea. Occ. Papers Calif. Acad. Sci., **7**, 262 pp., 4 pls., 2 figs. in text.

EXPLANATION OF PLATE 9

1. *Siriella pacifica* Holmes

Fig. 1*a*. Anterior part of an adult male, from above. × 20.

Fig. 1*b*. Left eye of the male, from the outer side. × 22.

Fig. 1*c*. Terminal parts of both rami of fourth right pleopod. × 82 *en*, endopod; *ex*, exopod.

Fig. 1*d*. End of abdomen with left uropod of the male, from above. × 20.

Fig. 1*e*. Distal portion of the telson shown in figure 1*d*, from above. × 67.

Fig. 1*f*. Front end of carapace with eyes of a female, from above. × 22.

2. *Mysis costata* Holmes

Fig. 2*a*. Distal part of left antennal squama, from below. × 52.

Fig. 2*b*. Fifth and sixth abdominal segments of a female, from above. × 22, *V*, fifth segment; *VI*, sixth segment.

Fig. 2*c*. Telson of a female, from above. × 34.

Fig. 2*d*. Distal portion of the same telson, from above. × 52.

3. *Neomysis franciscorum* Holmes

Fig. 3*a*. Anterior part of the type-specimen, from above. × 19⅓.

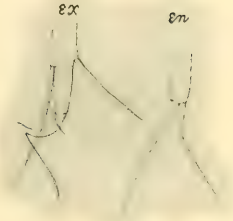
Fig. 3*b*. Telson of the type-specimen, from above. × 11.

1d

1a

1e

1f



1c

1b

2b

2d

2a

2c

3a

3b

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY
Vol. 11, No. 10, pp. 181-196, pls. 10-12 November 26, 1913

FOURTH TAXONOMIC REPORT
ON THE
COPEPODA OF THE SAN DIEGO REGION

BY
CALVIN O. ESTERLY

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY

UNIVERSITY OF CALIFORNIA PUBLICATIONS

Note.—The University of California Publications are offered in exchange for the publications of learned societies and institutions, universities and libraries. Complete lists of all the publications of the University will be sent upon request. For sample copies, lists of publications or other information, address the Manager of the University Press, Berkeley, California, U. S. A. All matter sent in exchange should be addressed to The Exchange Department, University Library, Berkeley, California, U. S. A.

OTTO HARRASSOWITZ, LEIPZIG.

Agent for the series in American Archaeology and Ethnology, Classical Philology, Education, Modern Philology, Philosophy, Psychology, History.

R. FRIEDLAENDER & SOHN, BERLIN.

Agent for the series in American Archaeology and Ethnology, Botany, Geology, Geography, Mathematics, Pathology, Physiology, Zoology, and Memoirs.

ZOOLOGY.—W. E. Ritter and C. A. Kofoid, Editors. Price per volume, $3.50. Commencing with Volume II, this series contains Contributions from the Laboratory of the Marine Biological Association of San Diego.

Cited as Univ. Calif. Publ. Zool.

Volume 1, 1902-1905, 317 pages, with 28 plates $3.50

Volume 2 (Contributions from the Laboratory of the Marine Biological Association of San Diego), 1904-1906, xvii + 382 pages, with 19 plates $3.50

Volume 3, 1906-1907, 383 pages, with 23 plates $3.50

Volume 4, 1907-1908, 400 pages, with 24 plates $3.50

Volume 5, 1908-1910, 440 pages, with 34 plates $3.50

Vol. 6.

1. (XXIII) On the Weight of Developing Eggs. Part I, The Possible Significance of Such Investigations, by William E. Ritter; Part II, Practicability of the Determinations, by Samuel E. Bailey. Pp. 1-10. October, 1908 ..... .10
2. (XXIV) The Leptomedusae of the San Diego Region, by Harry Beal Torrey. Pp. 11-31, with 11 text-figures. February, 1909 ..... .20
3. (XXV) The Ophiurans of the San Diego Region, by J. F. McClendon. Pp. 33-64, plates 1-6. July, 1909 ..... .30
4. (XXVI) *Halocynthia johnsoni* n. sp.: A comprehensive inquiry as to the extent of law and order that prevails in a single animal species, by Wm. E. Ritter. Pp. 65-114, plates 7-14. November, 1909 ..... .50
5. (XXVII) Three Species of *Cerianthus* from Southern California, by H. B. Torrey and F. L. Kleeberger. Pp. 115-125, 4 text-figures. December, 1909 ..... .10
6. The Life History of *Trypanosoma dimorphon* Dutton & Todd, by Edward Hindle. Pp. 127-144, plates 15-17, 1 text-figure. December, 1909 ..... .50
7. (XXVIII) A Quantitative Study of the Development of the Salpa Chain in *Salpa fusiformis-runcinata*, by Myrtle Elizabeth Johnson. Pp. 145-176. March, 1910 ..... .35
8. A Revision of the Genus *Ceratocorys*, Based on Skeletal Morphology, by Charles Atwood Kofoid. Pp. 177-187. May, 1910 ..... .10
9. (XXIX) Preliminary Report on the Hydrographic Work Carried on by the Marine Biological Station of San Diego, by George F. McEwen. Pp. 189-204; text-figure and map. May, 1910 ..... .15
10. (XXX) Biological Studies on *Corymorpha*. III, Regeneration of Hydranth and Holdfast, by Harry Beal Torrey. Pp. 205-221; 16 text-figures.
11. (XXXI) Note on Geotropism in *Corymorpha*, by Harry Beal Torrey. Pp. 223-224; 1 text-figure.
    Nos 10 and 11 in one cover. August, 1910 ..... .20
12. The Cyclostomatous Bryozoa of the West Coast of North America, by Alice Robertson. Pp. 225-284; plates 18-25. December, 1910 ..... .60
13. Significance of White Markings in Birds of the Order Passeriformes, by Henry Chester Tracy. Pp. 285-312. December, 1910 ..... .25
14. (XXXIII) Third Report on the Copepoda of the San Diego Region, by Calvin Olin Esterly. Pp. 313-352; plates 26-32. February, 1911 ..... .40
15. The Genus *Gyrocotyle*, and Its Significance for Problems of Cestode Structure and Phylogeny, by Edna Earl Watson. Pp. 353-468; plates 33-48. June, 1911 ..... 1.00

Index, pp. 469-478.

---

*Roman numbers indicate sequence of the Contributions from the Laboratory of the Marine Biological Association of San Diego.

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY
Vol. 11, No. 10, pp. 181-196, pls. 10-12 November 26, 1913

FOURTH TAXONOMIC REPORT
ON THE
COPEPODA OF THE SAN DIEGO REGION

BY
CALVIN O. ESTERLY

The copepods described here have been found since the last report was published (Esterly, 1911). With one exception the forms are regarded as new, though some are represented by single specimens. It should be understood, however, that in such cases the descriptions are more or less tentative, since they may need modification if more material is obtained; there is no intention of stating more than is known at present, that is, that the one animal differs from those which represent other species to such a degree that the formation of a new species is advisable. Experience has shown that additional material confirms the conclusion as to specific rank based on a single specimen, and it is unlikely that we are dealing in any of these cases with an individual variation that is without specific value.

The descriptions given are brief, and the figures do not cover all parts, but it is believed that they provide for the recognition of the forms discussed. The hauls in which the animals were found are given by number, and the complete data for the hauls will be found in a publication of the Scripps Institution now in course of preparation.

LIST OF SPECIES

PAGE
Arietellus pacificus n. sp. 189
Augaptilus californicus n. sp. 186
Augaptilus depressus n. sp. 187
Augaptilus romanus n. sp. 188
Augaptilus simplex n. sp. 188
Euchaeta elongata n. sp. 183
Gaetanus ascendens n. sp. 182
Onchocalanus latus Esterly 183
Scolecithrix aculeata n. sp. 183
Scolecithrix elephas n. sp. 185
Scolecithrix longirostris n. sp. 185
Scolecithrix mollis n. sp. 186
Scolecithrix obscura n. sp. 184

Gaetanus ascendens n. sp.

Pl. 10, figs. 1, 3, 6; pl. 11, fig. 39; pl. 12, fig. 56

Adult female. The cephalic spine is short and directed downward, and the rostrum is rather prominent for this genus (pl. 10, fig. 6). The spines on the last segment of the thorax are heavy and pointed toward the dorsal surface of the animal (pl. 10, figs. 1, 3). The proportions of the abdominal segments may be seen in plate 10, figures 1 and 3. The anterior antennae are a little longer than the cephalothorax. The first joint of the posterior maxilliped has the characteristic lamella of the shape and size indicated in plate 11, figure 39. The first foot has specific characters (so far as the forms of this region are concerned; pl. 12, fig. 56), and the first basal of the fourth foot has the row of hair-like spines.

Length: 3.7 mm. (cephalothorax, 3 mm.).

Coloration: Unpigmented and rather opaque in formalin.

Occurrence: Haul 1524.

Euchaeta elongata n. sp.

Pl. 10, figs. 5, 16, 27; pl. 11, fig. 37; pl. 12, fig. 49

Adult female. The head and rostrum in profile (pl. 10, fig. 16) have a characteristic shape; the rostrum is heavy and straight, pointing obliquely down; the frontal hairs are not situated on a noticeable papilla. The sides of the last thoracic segment are not broadly rounded, but end in blunt projection (pl. 10, figs.

5, 27). The genital segment has a characteristic form (pl. 10, figs. 5, 27); it is not symmetrical; the ventral surface is markedly protuberant, with a lamella at the right of the orifice. The figures give a better idea of the form of the segment than is possible in a description.

The anterior antennae are slightly longer than the cephalothorax. In the second foot, the outer marginal spine on the end of the second joint of the outer ramus reaches nearly to the tip of the first spine of the last joint; the middle spine of the third joint is long and extends to the distal margin of the joint, but the proximal and distal spines are short (pl. 11, fig. 37). The outer ramus of the first two (pl. 12, fig. 49) is 2-jointed, though there is some indication of the suture between the first and second joints; the outer margin of the proximal division of the ramus is deeply concave and bears one spine, which reaches to the end of the distal division.

Length: 4.13 mm. (cephalothorax 2.95 mm.).

Coloration: Translucent and whitish in formalin.

Occurrence: Haul 2258.

Onchocalanus latus Esterly

Pl. 10, figs. 13, 15; pl. 12, fig. 58

Drawings are given here to supplement those previously shown (see Esterly, 1911, p. 326). It is certain that this species does not possess a fifth pair of feet, though I stated in the passage just cited that it was lost through mutilation; the specimen described as *O. latus* meet the description of *Onchocalanus* as given by Sars (1905a, p. 18) and by Farran (1906, p. 49) in important requirements notwithstanding the absence of the fifth pair of feet.

The animal figured in this paper was 4.3 mm. in length and was taken in haul 2134.

Scolecithrix aculeata n. sp.

Pl. 10, figs. 2, 25; pl. 12, figs. 63, 64

Adult female. The head is rounded and further characterized by the bifid rostrum, each prong of which is heavy at the base and carries a delicate but stiff and sharp spine at the distal end

(pl. 10, fig. 25). The last segment of the thorax is rounded at the sides and the dorsal margin of the segment is slightly concave (pl. 10, fig. 2). The abdomen is 4-segmented; the genital segment is nearly as long as the second, third, and fourth together; the fourth segment is short, about one-tenth the length of the first segment (pl. 10, fig. 2).

The anterior maxilliped has four pencillate sensory appendages; the others are vermiform. The outer ramus of the first foot is shown in plate 12, figure 64. The fifth foot is 3-jointed; the distal margins of the first two joints have rows or groups of fine spines; the third joint carries a long heavy spine on the inner margin and a shorter one on the distal end, both set with small teeth or spines (pl. 12, fig. 63).

Length: 1.8 mm. (cephalothorax 1.35 mm.).

Coloration: Translucent in formalin.

Occurrence: Haul 2567.

Scolecithrix obscura n. sp.

Pl. 10, figs. 18, 21; pl. 11, fig. 35; pl. 12, figs. 53, 57

Adult female. The head is smoothly rounded and distinctly crested; the rostral filaments are exceedingly delicate (pl. 10, fig. 21). The last segment of the thorax ends on each side in a minute point which is located on the ventral border (pl. 10, fig. 18). The head is fused with the first thoracic segment. The abdomen is 4-segmented and the segments and furca are of about equal lengths (pl. 10, fig. 18).

The anterior maxilliped, as shown in plate 11, figure 35, bears four vermiform appendages and five with tufts at the end. The first foot has a 3-jointed outer ramus, the second joint bearing a very minute spine at the distal end of the outer margin; the third joint has a heavy and much longer spine in that position (pl. 12, fig. 53). The fifth foot is 3-jointed; the third joint has two large spines (one on the inner margin and one at the end) and two minute spines, of which one is at the end of the joint, the other at about the middle of the outer margin (pl. 12, fig. 57).

Length: 2.5 mm. (cephalothorax 1.95 mm.).

Coloration: Rather opaque and without pigment in formalin.

Occurrence: Haul 2134.

Scolecithrix elephas n. sp.

Pl. 10, figs. 8, 17; pl. 12, figs. 59, 62

Adult female. The species may be easily recognized by the shape of the head in profile (pl. 10, fig. 8); the rostrum is bifid and remarkably long and heavy in the basal two-thirds, with a delicate filament at the end. The drawing in plate 10, figure 17, shows the shape of the last thoracic segment and the proportions of the abdominal segments.

The anterior antennae are 23-jointed and 1.6 mm. long. The outer ramus of the first foot is shown in figure 59 and the fifth foot in figure 62 of plate 12. The third joint of the fifth foot tapers to an awl-like point; the outer margin near the base carries a small spine, and there is a heavy toothed bristle on the inner margin of the joint. There is a row of seven or eight spines on the distal margin of the second joint.

Length: 1.6 mm. (cephalothorax 1.2 mm.).

Coloration: Semi-transparent and without pigment.

Occurrence: Haul 2002.

Scolecithrix longirostris n. sp.

Pl. 10, figs. 12, 19; pl. 12, fig. 51

Adult female. The head is smoothly rounded, with a very long, heavy rostrum (pl. 12, fig. 19). The sides of the last thoracic segment are broadly rounded, as shown in plate 10, figure 12, which also serves to indicate the proportional lengths of the abdominal segments. The head is fused with the thorax and there is no line between the fourth and fifth segments of the thorax.

The anterior antennae are 23-jointed and 1.8 mm. long. The other appendages of the head do not present noticeable features; the maxillipeds are broken. The outer ramus of the first foot (pl. 12, fig. 51) is distinctive; there is no trace of a fifth foot.

Length: 2.07 mm. (cephalothorax 1.6 mm.).

Coloration: Without pigment and somewhat translucent.

Occurrence: Haul 2134.

Scolecithrix mollis n. sp.

Pl. 10, figs. 14, 29; pl. 12, figs. 62, 65

Adult female. The head is rounded; the rostrum is bifid, with soft and rather delicate filaments of a characteristic shape (pl. 10, fig. 29). The last thoracic segment has rounded lateral margins, the dorsal portion of the outline being indented, as shown in plate 10, figure 14. The genital segment of the abdomen is about as long as the second and third together, and four times as long as the fourth (pl. 10, fig. 14).

The outer ramus of the first foot exhibits specific characters (pl. 12, fig. 65). The fifth foot (pl. 12, fig. 62) is 2-jointed; the second joint has a short, heavy spine on the distal end, a very heavy dentate bristle at the middle of the inner margin, and two tiny spines, one at the end of the joint, the other at the middle of the outer margin.

Length: 1.55 mm. (cephalothorax about 1 mm.).

Coloration: Unpigmented and opaque in formalin.

Occurrence: Haul 2567.

Augaptilus californicus n. sp.

Pl. 10, figs. 4, 22; pl. 11, figs. 31, 40; pl. 12, figs. 43, 48

Adult female. The body is somewhat flattened. The head is rounded and carries the stiff, bifid rostrum on a projecting, fleshy eminence (pl. 10, fig. 22). The last segment of the thorax is rounded laterally and the cephalothorax is four and one-half times as long as the abdomen. The genital segment protrudes a good deal on the ventral surface and the aperture is surrounded by hairs; the segment is as long as the other two together and more than three times as long as the second segment (pl. 10, fig. 4).

The anterior antennae are 24-jointed, and are 7.3 mm. long. The inner ramus of the posterior antennae (pl. 11, fig. 40) is less than twice the length of the outer. The blade of the mandible is elongated; the arrangement of teeth on it is shown in plate 11, figure 31. The maxillipeds have distinctly cupped bristles.

The feet do not show characters that are easily described, but the outer ramus of the first foot, and the fifth foot, are

figured in plate 12, figures 43 and 48 respectively; these appendages have readily recognizable specific structures so far as the members of the genus in this region are concerned.

Length: 5.8 mm. (cephalothorax 5 mm.).

Coloration: Very transparent; there is a brown band around the twentieth joint of the anterior antennae.

Occurrence: Haul 2081.

Augaptilus depressus n. sp.

Pl. 10, figs. 11, 20, 26; pl. 11, figs. 33, 38, 42; pl. 12, figs. 44, 54

Adult female. The body is greatly flattened, with rounded head and posterior margins of the thorax; the rostral filaments are unusually long and delicate, and recurved (pl. 10, fig. 11). The cephalothorax is four and one-third times as long as the abdomen, including the furca, and nearly four times as long as the greatest breadth; the greatest width in the median sagittal plane is half that in the frontal plane. In the abdomen (pl. 10, fig. 20) the genital segment is longer than the other two segments with the furca; the genital segment is also about five times as long as the second segment and the latter is somewhat shorter than the third.

The anterior antennae are not quite so long as the cephalothorax. The inner ramus of the posterior antennae is about twice as long as the outer and extends back half way to the posterior edge of the cephalothorax; the larger plumose bristles are iridescent. The blade of the mandible is shown in plate 11, figure 33; figures 38 and 42 are outlines of the anterior and posterior antennae respectively, without the bristles. The bristles of the maxillipeds are provided with the "buttons" which are exceedingly minute; only about the distal eighth of any bristle is so equipped; the remainder of the bristles is spinose.

The outer ramus of the first foot is shown in plate 12, figure 44, and the fifth foot in figure 54; both have specific characters.

Length: 5.3 mm. (cephalothorax 4.3 mm.).

Coloration: Transparent, except for the digestive tract filled with light yellowish material; the plumose bristles of the antennae and furca are iridescent.

Occurrence: Haul 2068.

Augaptilus romanus n. sp.

Pl. 10, figs. 7, 24; pl. 11, figs. 30, 32; pl. 12, figs. 45, 47, 52

Adult male. The body is much depressed, and the head and posterior margins of the last thoracic segment are rounded. The rostral filaments are slender and delicate and borne on a prominent beak-like eminence which is set in an indentation in the front of the head (pl. 10, fig. 24). The cephalothorax is about four times as long as the abdomen and furca.

The last segment is the longest of the abdomen and the genital segment is next, then the second, third, and fourth in order (pl. 10, fig. 7).

The non-grasping antenna is 25 jointed and 5.4 mm. long; the portion of the grasping antenna proximal to the geniculation is 17-jointed (the rest was broken off). The inner ramus of the posterior antenna is twice the length of the outer ramus (pl. 11, fig. 30). The blade of the mandible is shown in plate 11, figure 32. The bristles of the maxillipeds have the buttons, and the posterior maxilliped is extremely long and slender. The outer ramus of the first foot (pl. 12, fig. 45) has distinctive characters; the fifth feet, also (pl. 12, figs. 47, 52) are easily recognizable from the figures.

Length: 4.5 mm.

Coloration: Transparent and unpigmented.

Occurrence: Haul 2081.

While this specimen was taken in the same haul with *A. californicus*, there is no other reason, so far as I can see, for considering the two as male and female of the same species.

Augaptilus simplex n. sp.

Pl. 10, figs. 10, 28; pl. 11, figs. 34, 36, 41; pl. 12, figs. 50, 60

Adult female. The head is regularly and broadly rounded; there are no rostral filaments, but the rostrum appears to be represented by a nodular protuberance, the lower one of the two shown in plate 10, figure 28. The last thoracic segment is rounded at the sides; the cephalothorax is about four and one-

half times as long as the abdomen and furca. The genital segment is markedly protuberant on the ventral border; this segment is as long as the rest of the abdomen and the furca (pl. 10, fig. 10).

The anterior antennae are 24-jointed and slightly longer than the cephalothorax. The inner ramus of the posterior antennae is between two and three times as long as the outer. The mandibular blade is shown in plate 11, figure 34, and the anterior and posterior maxillipeds in figures 41 and 36 respectively. The bristles of the maxillipeds do not have the cups or "buttons" so generally found in this genus. The feet do not appear to be unusual. Figures 50 and 60 of plate 3 show the outer ramus of the first foot and the fifth foot respectively.

Length: 6.1 mm. (cephalothorax 5 mm.).

Coloration: Transparent, but the plumose bristles of the posterior antennae and the mandible and those of the furca are iridescent.

Occurrence: Hauls 1524 and 2569.

This species appears to resemble *A. nodifrons* (Sars, 1905, p. 13), which is also arostrate and without the buttons on the bristles of the maxillipeds.

Arietellus pacificus n. sp.

Pl. 10, figs. 9, 23; pl. 12, figs. 46, 55

Adult female. The head is smoothly rounded, with an inconspicuous crest. The rostral filaments are delicate but straight and rather stiff (pl. 10, fig. 9). The sides of the last thoracic segment are rounded, as shown in plate 10, figure 23; this figure also shows the proportionate lengths of the abdominal segments and furca.

The anterior antennae are 19-jointed, and as carried on the body reach to the posterior border of the second thoracic segment. The first joint of the antenna is as long as the next eight together. The outer ramus of the first foot (pl. 12, fig. 46) shows distinctive characters. The fifth foot (pl. 12, fig. 55) is also of use in the recognition of the species.

Length: 4.5 mm. (cephalothorax 3.6 mm.).
Coloration: Opaque and without pigment.
Occurrence: Haul 1524.

Occidental College, Los Angeles, California.

Transmitted September 11, 1913.

BIBLIOGRAPHY

Esterly, C. O.
1911. Third report on the Copepoda of the San Diego Region. Univ. Calif. Publ. Zool., **6**, 313–352, pls. 26–32.

Farran, G. P.
1906. Second report on the Copepoda of the Irish Atlantic Slope. Dept. of Agr. and Tech. Instr. for Ireland, Fisheries Branch, Sci. Invest., **1906**, 3–104, pls. 1–11.

Sars, G. O.
1905. Liste préliminaire des Calanoidés recueillis pendant les Campagnes de S. A. S. le Prince Albert de Monaco. 2me Partie.

EXPLANATION OF PLATES

PLATE 10

Fig. 1. *Gaetanus ascendens* n. sp. Female, abdomen and part of last thoracic segment, from side. × 35.

Fig. 2. *Scolecithrix aculeata* n. sp. Female, abdomen and part of thorax, from side. × 70.

Fig. 3. *Gaetanus ascendens* n. sp. Female, abdomen and part of last thoracic segment, from above. × 35.

Fig. 4. *Augaptilus californicus* n. sp. Female, abdomen, from side. × 35.

Fig. 5. *Euchaeta elongata* n. sp. Female, genital segment and tip of last thoracic segment, from below. × 35.

Fig. 6. *Gaetanus ascendens* n. sp. Female, anterior part of head, from side. × 35.

Fig. 7. *Augaptilus romanus* n. sp. Male, abdomen, from above. × 35.

Fig. 8. *Scolecithrix elephas* n. sp. Female, anterior part of head, from side. × 35.

Fig. 9. *Arietellus pacificus* n. sp. Female, anterior part of head, from side. × 70.

Fig. 10. *Augaptilus simplex* n. sp. Female, abdomen, from below. × 22.

Fig. 11. *Augaptilus depressus* n. sp. Female, forehead, from side. × 35.

Fig. 12. *Scolecithrix longirostris* n. sp. Female, abdomen and last segment of thorax, from side. × 35.

Fig. 13. *Onchocalanus latus* Esterly. Female, abdomen and part of thorax, from side. × 35.

Fig. 14. *Scolecithrix mollis* n. sp. Female, abdomen and last segment of thorax, from side. × 35.

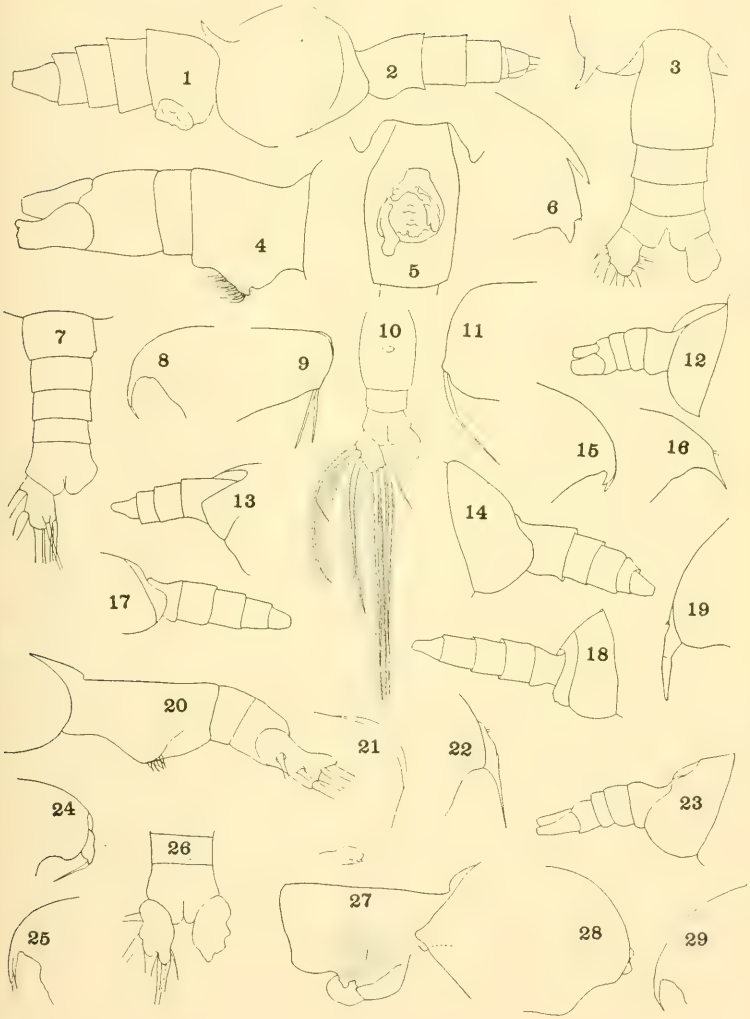
Fig. 15. *Onchocalanus latus* Esterly. Female, forehead, from side. × 35.

Fig. 16. *Euchaeta elongata* n. sp. Female, forehead, from side. × 35.

Fig. 17. *Scolecithrix elephas* n. sp. Female and posterior part of thorax, from side. × 35.

Fig. 18. *Scolecithrix obscura* n. sp. Female, abdomen and last two thoracic segments, from side. × 35.

Fig. 19. *Scolecithrix longirostris* n. sp. Female, forehead, from side. × 70.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29

EXPLANATION OF PLATE 10—*Continued*

Fig. 20. *Augaptilus depressus* n. sp. Female, abdomen, from side. × 35.

Fig. 21. *Scolecithrix obscura* n. sp. Female, forehead, from side. × 70.

Fig. 22. *Augaptilus californicus* n. sp. Female, forehead, from side. × 35.

Fig. 23. *Arietellus pacificus* n. sp. Female, abdomen and last segment of thorax, from side. × 35.

Fig. 24. *Augaptilus romanus* n. sp. Female, forehead, from side. × 35.

Fig. 25. *Scolecithrix aculeata* n. sp. Female, forehead, from side. × 35.

Fig. 26. *Augaptilus depressus* n. sp. Female, second and third segments of abdomen, and furca, from above. × 35.

Fig. 27. *Euchaeta elongata* n. sp. Female, genital segment and tip of thorax, from side. × 35.

Fig. 28. *Augaptilus simplex* n. sp. Female, forehead, from side. × 22.

Fig. 29. *Scolecithrix mollis* n. sp. Female, forehead, from side. × 35.

PLATE 11

Fig. 30. *Augaptilus romanus* n. sp. Male, posterior antenna. × 47.

Fig. 31. *Augaptilus californicus* n. sp. Female, mandibular blade. × 93.

Fig. 32. *Augaptilus romanus* n. sp. Male, mandibular blade. × 145.

Fig. 33. *Augaptilus depressus* n. sp. Female, mandibular blade. × 145.

Fig. 34. *Augaptilus simplex* n. sp. Female, mandibular blade. × 93.

Fig. 35. *Scolecithrix obscura* n. sp. Female, sensory appendages of anterior maxilliped. × 145.

Fig. 36. *Augaptilus simplex* n. sp. Female, posterior maxilliped. × 30.

Fig. 37. *Euchaeta elongata* n. sp. Female, second and third joints of outer ramus of second foot. × 47.

Fig. 38. *Augaptilus depressus* n. sp. Female, outline of anterior maxilliped without the bristles. × 47.

Fig. 39. *Gaetanus ascendens* n. sp. Female, first basal of posterior maxilliped. × 93.

Fig. 40. *Augaptilus californicus* n. sp. Female, posterior antenna. × 47.

Fig. 41. *Augaptilus simplex* n. sp. Female, anterior maxilliped. × 47.

Fig. 42. *Augaptilus depressus* n. sp. Female, outline of posterior maxilliped without the bristles. × 47.

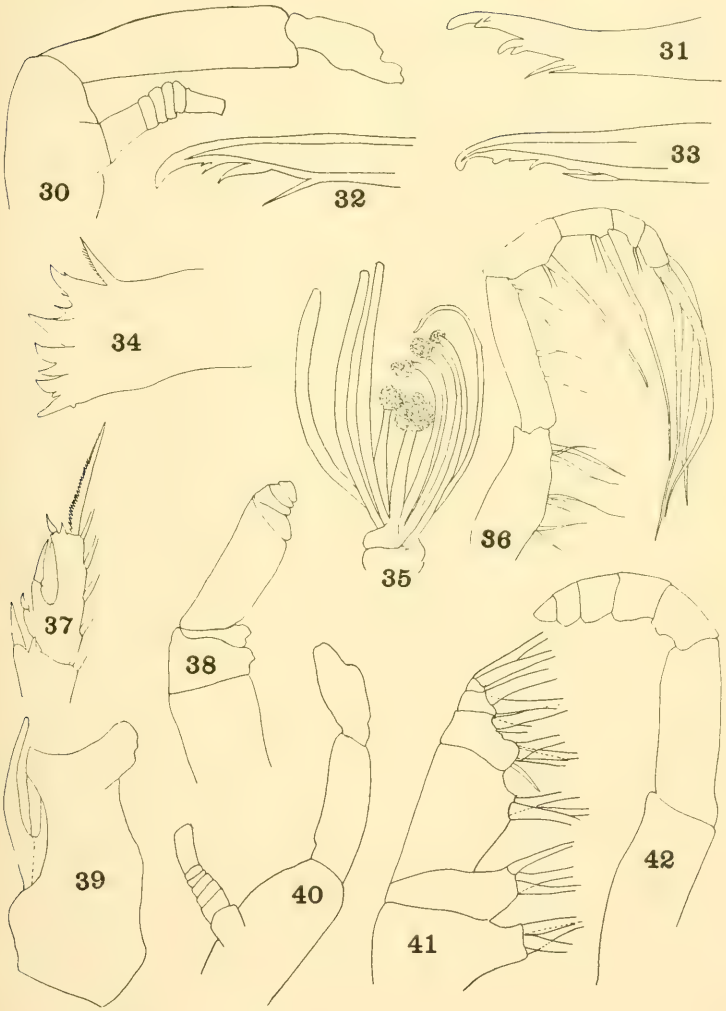

30
31
32
33
34
35
36
37
38
39
40
41
42

PLATE 12

Fig. 43. *Augaptilus californicus* n. sp. Female, outer ramus of first foot. × 70.

Fig. 44. *Augaptilus depressus* n. sp. Female, outer ramus of first foot. × 70.

Fig. 45. *Augaptilus romanus* n. sp. Male, outer ramus of first foot. × 70.

Fig. 46. *Arietellus pacificus* n. sp. Female, first foot. × 35.

Fig. 47. *Augaptilus romanus* n. sp. Male, right fifth foot. × 70.

Fig. 48. *Augaptilus californicus* n. sp. Female, fifth foot. × 35.

Fig. 49. *Euchaeta elongata* n. sp. Female, outer ramus of first foot. × 70.

Fig. 50. *Augaptilus simplex* n. sp. Female, outer ramus of first foot. × 35.

Fig. 51. *Scolecithrix longirostris* n. sp. Female, first foot without inner ramus. × 70.

Fig. 52. *Augaptilus romanus* n. sp. Male, left fifth foot. × 70.

Fig. 53. *Scolecithrix obscura* n. sp. Female, outer ramus of first foot. × 70.

Fig. 54. *Augaptilus depressus* n. sp. Female, fifth foot. × 70.

Fig. 55. *Arietellus pacificus* n. sp. Female, fifth foot. × 70.

Fig. 56. *Gaetanus ascendens* n. sp. Female, outer ramus of first foot. × 70.

Fig. 57. *Scolecithrix obscura* n. sp. Female, fifth foot. × 188.

Fig. 58. *Onchocalanus latus* Esterly. Female, outer ramus of first foot. × 70.

Fig. 59. *Scolecithrix elephas* n. sp. Female, outer ramus of first foot. × 90.

Fig. 60. *Augaptilus simplex* n. sp. Female, fifth foot. × 35.

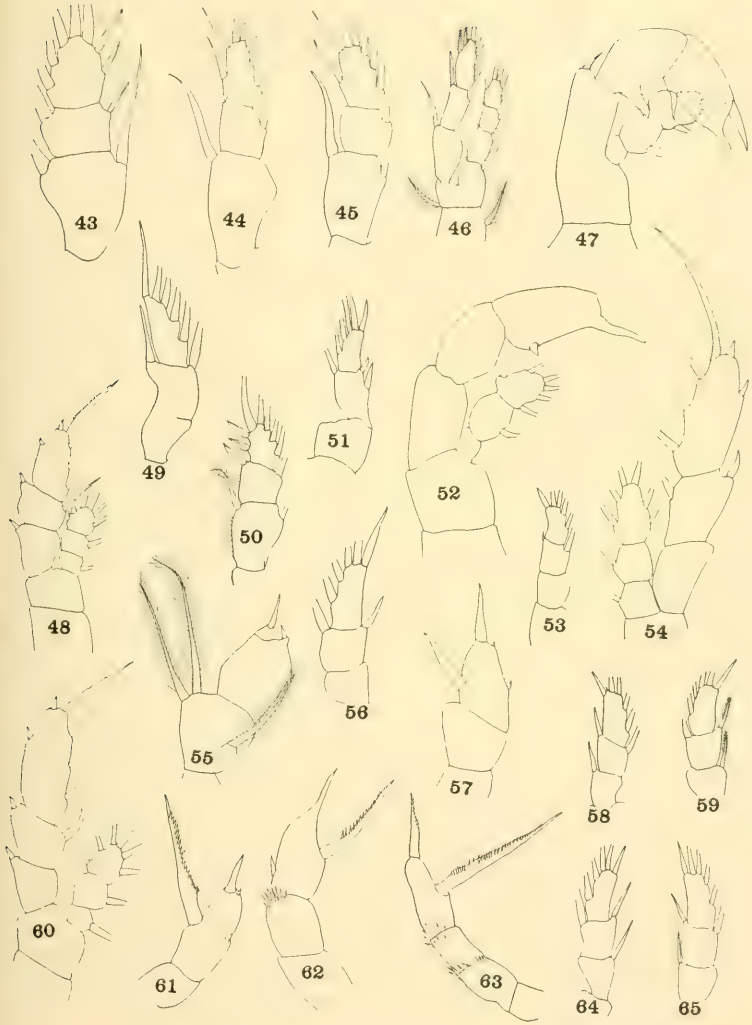
Fig. 61. *Scolecithrix aculeata* n. sp. Female, fifth foot. × 188.

Fig. 62. *Scolecithrix elephas* n. sp. Female, fifth foot. × 250.

Fig. 63. *Scolecithrix aculeata* n. sp. Female, fifth foot. × 188.

Fig. 64. *Scolecithrix aculeata* n. sp. Female, outer ramus of first foot. × 70.

Fig. 65. *Scolecithrix mollis* n. sp. Female, outer ramus of first foot. × 93.


43
44
45
46
47
49
51
52
48
50
53
54
55
56
57
58
59
60
61
62
63
64
65

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY
Vol. 11, No. 11, pp. 197-305, 13 text figures. December 9, 1913

THE BEHAVIOR OF LEECHES WITH ESPECIAL REFERENCE TO ITS MODIFIABILITY

A. THE GENERAL REACTIONS OF THE LEECHES *DINA MICROSTOMA* MOORE AND *GLOSSIPHONIA STAGNALIS* LINNAEUS

B. MODIFIABILITY IN THE BEHAVIOR OF THE LEECH *DINA MICROSTOMA* MOORE

BY
WILSON GEE

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY

Note.—The University of California Publications are offered in exchange for the publications of learned societies and institutions, universities and libraries. Complete lists of all the publications of the University will be sent upon request. For sample copies, lists of publications or other information, address the Manager of the University Press, Berkeley, California, U. S. A. All matter sent in exchange should be addressed to The Exchange Department, University Library, Berkeley, California, U. S. A.

OTTO HARRASSOWITZ, LEIPZIG.

Agent for the series in American Archaeology and Ethnology, Classical Philology, Education, Modern Philology, Philosophy, Psychology, History.

E. FRIEDLAENDER & SOHN, BERLIN.

Agent for the series in American Archaeology and Ethnology, Botany, Geology, Geography, Mathematics, Pathology, Physiology, Zoology, and Memoirs.

ZOOLOGY.—W. E. Ritter and C. A. Kofoid, Editors. Price per volume, $3.50. Commencing with Volume II, this series contains Contributions from the Laboratory of the Marine Biological Association of San Diego.

Cited as Univ. Calif. Publ. Zool.

Volume 1, 1902-1905, 317 pages, with 28 plates $3.50

Volume 2 (Contributions from the Laboratory of the Marine Biological Association of San Diego), 1904-1906, xvii + 382 pages, with 19 plates $3.50

Volume 3, 1906-1907, 383 pages, with 23 plates $3.50

Volume 4, 1907-1908, 400 pages, with 24 plates $3.50

Volume 5, 1908-1910, 440 pages, with 34 plates $3.50

Vol. 6. 1. (XXIII) On the Weight of Developing Eggs. Part I, The Possible Significance of Such Investigations, by William E. Ritter; Part II, Practicability of the Determinations, by Samuel E. Bailey. Pp. 1-10. October, 1908 ..... .10

2. (XXIV) The Leptomedusae of the San Diego Region, by Harry Beal Torrey. Pp. 11-31, with 11 text-figures. February, 1909 ..... .20

3. (XXV) The Ophiurans of the San Diego Region, by J. F. McClendon. Pp. 33-64, plates 1-6. July, 1909 ..... .30

4. (XXVI) *Halocynthia johnsoni* n. sp.: A comprehensive inquiry as to the extent of law and order that prevails in a single animal species, by Wm. E. Ritter. Pp. 65-114, plates 7-14. November, 1909 ..... .50

5. (XXVII) Three Species of *Cerianthus* from Southern California, by H. B. Torrey and F. L. Kleeberger. Pp. 115-125, 4 text-figures. December, 1909 ..... .10

6. The Life History of *Trypanosoma dimorphon* Dutton & Todd, by Edward Hindle. Pp. 127-144, plates 15-17, 1 text-figure. December, 1909 ..... .50

7. (XXVIII) A Quantitative Study of the Development of the Salpa Chain in *Salpa fusiformis-runcinata*, by Myrtle Elizabeth Johnson. Pp. 145-176. March, 1910 ..... .35

8. A Revision of the Genus *Ceratocorys*. Based on Skeletal Morphology, by Charles Atwood Kofoid. Pp. 177-187. May, 1910 ..... .10

9. (XXIX) Preliminary Report on the Hydrographic Work Carried on by the Marine Biological Station of San Diego, by George F. McEwen. Pp. 189-204; text-figure and map. May, 1910 ..... .15

10. (XXX) Biological Studies on *Corymorpha*. III, Regeneration of Hydranth and Holdfast, by Harry Beal Torrey. Pp. 205-221; 16 text-figures.

11. (XXXI) Note on Geotropism in *Corymorpha*, by Harry Beal Torrey. Pp. 223-224; 1 text-figure.

Nos 10 and 11 in one cover. August, 1910 ..... .20

12. The Cyclostomatous Bryozoa of the West Coast of North America, by Alice Robertson. Pp. 225-284; plates 18-25. December, 1910 ..... .60

13. Significance of White Markings in Birds of the Order Passeriformes, by Henry Chester Tracy. Pp. 285-312. December, 1910 ..... .25

14. (XXXIII) Third Report on the Copepoda of the San Diego Region, by Calvin Olin Esterly. Pp. 313-352; plates 26-32. February, 1911 ..... .40

15. The Genus *Gyrocotyle*, and Its Significance for Problems of Cestode Structure and Phylogeny, by Edna Earl Watson. Pp. 353-468; plates 33-48. June, 1911 ..... 1.00

Index, pp. 469-478.

*Roman numbers indicate sequence of the Contributions from the Laboratory of the Marine Biological Association of San Diego.

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY

Vol. 11, No. 11, pp. 197-305, 13 text figures. December 9, 1913

THE BEHAVIOR OF LEECHES WITH ESPECIAL REFERENCE TO ITS MODIFIABILITY

A. THE GENERAL REACTIONS OF THE LEECHES *DINA MICROSTOMA* MOORE AND *GLOSSIPHONIA STAGNALIS* LINNAEUS

B. MODIFIABILITY IN THE BEHAVIOR OF THE LEECH *DINA MICROSTOMA* MOORE

BY

WILSON GEE

CONTENTS

PAGE

A. The General Reactions of the Leeches *Dina microstoma* Moore and *Glossiphonia stagnalis* Linnaeus.
I. Introduction 199
II. Resumé of literature 199
III. Description of material 206
IV. Categories of movements in leeches 208
1. Basis for classification 208
2. Random movements 209
3. Looping response 210
4. Swimming response 211
5. Undulatory respiratory movements 212
6. Righting reactions 214
V. General responses to stimuli 216
1. Formation of collections 216
2. Food of leeches 217
3. Feeding reactions 219
4. Sensitivity to various stimuli 221
5. Reactions to light 223
6. Effect of currents 227
7. Chemotactic responses 229
8. Reactions to gravity 230
9. Influence of heat 231
10. Thigmotaxis 232
11. Ability to withstand desiccation 232

PAGE

VI. Special features of behavior in leeches 233
1. Modification of behavior during breeding season 233
2. Diurnal rhythmical behavior 240
3. Behavior of the young leeches 241
4. Operation experiments 245
5. Function of the brain 248

B. Modifiability in the Behavior of the Leech *Dina microstoma* Moore.
I. Introduction 250
II. Different responses to the same stimulus 251
1. Reactions to stimulation of the anterior end 252
2. Order of response in twenty-five stimulations of the anterior end 254
3. Reactions to stimulation of posterior end 256
4. Determining factors of the different responses to the same stimulus 256
(*a*) Intensity of stimulus 256
(*b*) Localization of stimulus 257
(*c*) Position of the body 257
(*d*) Tonus of the organism 258
(*e*) Chain reflexes 259
III. Acclimatization to stimuli 261
1. Acclimatization to repeated jars 261
2. Acclimatization to successive shadows 263
3. General discussion of acclimatization results 265
IV. Normal fatigue from repeated contact stimuli 267
V. Induced depression 272
1. General methods 272
2. Strychnine 273
3. Nicotine 274
4. Cocaine 278
5. Chloretone 279
6. Magnesium sulphate 280
7. Carbon dioxide 282
8. Mono-potassium phosphate 283
9. Lactic acid 284
10. Discussion of fatigue 284
VI. Effect of combined stimuli 285
1. Influence of food-juices on reaction to contact in 285
(*a*) Normal individuals 285
(*b*) Starved leeches 287
(*c*) Well-fed leeches 288
2. Light and contact 288
VII. Influence of internal states 290
1. Behavior of well-fed leeches 290
2. Reactions of starved leeches 291
3. Responses of undisturbed leeches 292
VIII. General considerations on modifiability in leeches 295
IX. Summary 297
X. Bibliography 301

A. THE GENERAL REACTIONS OF THE LEECHES *DINA MICROSTOMA* MOORE AND *GLOSSIPHONIA STAGNALIS* LINNAEUS

I. INTRODUCTION

The work reviewed in this paper is the outgrowth of studies begun on the modifiability of behavior of leeches. Upon undertaking this problem the writer was impressed with the lack of work on the general reactions of the forms he wished to investigate. This deficiency was the stimulus productive of the general studies presented in the first part of this paper. A knowledge of the responses of the leeches made more efficient a detailed investigation of certain features of the modifiability of behavior of one of the species studied, *Dina microstoma* Moore. The second part of the paper is a consideration of the results of this investigation.

My chief debt of gratitude is to Professor S. J. Holmes for suggesting the problem, and for constant advice, criticism, and encouragement during the progress of the work. To Professor C. A. Kofoid I wish to acknowledge my appreciation of many courtesies extended. The identification of the material used was made by Professor J. Percy Moore of the University of Pennsylvania, and to him I desire to express my appreciation of the favor.

II. RESUMÉ OF LITERATURE

The contributions to leech literature are enormous in quantity and extend back to the middle ages. The interest in leeches manifested in this literature is very largely the outgrowth of the important part played by the blood-leech in early medical practice. That the estimated value of the animal was very much out of proportion to its real value is a fact too obvious for mention. In spite of the recognized fact that the leech is an agent for the transfer of blood parasites from one host to another, there still persists in the medical practice of today a use, fortunately diminishing, of the blood-leech.

It seems that Themison, the founder of the ancient medical sect of the Methodici, and an eminent physician of Laodicea, in Syria (circ. 100 B.C.), was the first to make use of leeches in medical practice. According to Houghton (1863), the ancient Hebrews and Orientals generally do not appear to have been acquainted with this method of blood-letting. Abundant evidence is available, however, that the Greeks and Romans were familiar with the practice and made use of it freely.

At one time the leeches were considered to be reliable weather prognosticators. If a wind was about to rise, "the poor prisoner galloped through its limpid habitation with amazing swiftness"; while, if a storm was at hand, the leech crawled up the side of the dish and, lodging out of the water, "discovered great uneasiness in violent throes and convulsions." So staunchly held were these views that experiments to test their validity were conducted by Valmont de Bomare (1776), Vitet (1809), and Bonnet (1775), which showed that the leeches were in no wise reliable weather indicators, nor were they likely, as was held by many, to replace the barometers of that period.

There is a striking meagreness of recent literature devoted to the behavior of the Hirudinea. The contributions of Darwin (1883), Hofmeister (1845), Parker (1901), Smith (1902), Adams (1903), Holmes (1905), Harper (1905), Jennings (1906), Yerkes (1912), and a number of others on the behavior of the earthworm have established so thoroughly the fundamental features of annelid behavior that it is perhaps for this reason that the leeches have been neglected. The most of the earlier literature has been found to deal largely with the questions of structure and classification, little attention being given to the natural history of the leeches.

Several extensive monographs have been devoted to the general considerations of leeches. The earliest of these of significance is that by Moquin-Tandon (1827). The same author several years later (1846) revised and enlarged his earlier work, and this revision constitutes a classic in the literature on leeches. Another extensive writer on leeches is Ebrard, to whose credit are two volumes: the first, *Des sangsues, considérées au point de vue de l'economie medicale* (1848); the second, *Nouvelle*

monographie des sangsues medicinales (1857). Within a period of one year (1854) Busquet, Fermond, and Laurens each published a somewhat extensive monograph on the subject of leeches. This fact is an excellent indication of the interest taken in leeches at that time. The volumes of the last four authors just mentioned have not been available, and, consequently, little can be said here with regard to the general nature of these contributions.

So far as I have been able to determine, the most significant of the earlier writers is Moquin-Tandon, who in his *Monographie de la famille des hirudinées* (1827, 1846) considers the sum total of the literature previous to his time, and discusses in a very interesting way the structure, habits, and classification of leeches, and to a considerable extent their use in medical practice and the breeding of them for commercial purposes. This volume contains a twenty-four page bibliography of the earlier literature, the titles extending back as far as the latter half of the seventeenth century. In the numbers of references on leeches which have been examined in connection with the work presented in this paper, none of the earlier writers has been found to be quoted nearly to the same extent as has Moquin-Tandon.

Brandt and Ratzeburg (1833) in their *Medizinische Zoologie* consider at some length the classification, anatomy, and the use of the blood-leech in the medical practice of the early part of the nineteenth century.

Houghton (1863) discusses his observations on the breeding habits and general behavior of the Glossiphonidae. Certain species of this family he describes as "incubating" their eggs; others as carrying the eggs attached to the ventral surface of the body, and later the young in the same position. Of *Glossiphonia tessulata* he observes: "I have counted a hundred and twenty young ones attached to the parent. The young for some little time after they are perfectly formed continue tied to their 'mother's apron-strings,' which they generally leave when they are about six weeks old." He correctly observes that leeches of this family "are incapable of swimming and move from place to place like the caterpillars called geometric." A somewhat later article (1863) by the same author, entitled "Leech-Lore," has been quoted in part in a preceding paragraph.

The locomotion, mechanism of biting, sucking, and swallowing in the blood-leech form the material for several short articles by Carlet (1883).

According to Whitman (1878), Grube (1844), in his work on the embryology of *Clepsine* (*Glossiphonia*), has discussed in a very general way the breeding habits of one of the species of this genus which carries its eggs in sacs under the body. This work has not been accessible, and mention only can be made of it.

The chief worker of more recent date on leeches has been Whitman. His interests were mainly morphological, and his contributions in that particular are substantial indeed. Many fragments of the natural history of various species of leeches we owe to his keen observation and interesting description. In one of the first of his papers on leeches (1878), which dealt with the embryology of *Clepsine,* he records some observations on the breeding behavior of *Clepsine marginata.* Under Whitman's supervision, Iijima (1882) made the only substantial observations which I have been able to find on the breeding behavior of a Nephelid. Iijima discovered what he misconstrued as abnormal copulation, but which was later interpreted by Whitman as fertilization by means of hypodermal impregnation accomplished through spermatophore attachment.

In his monograph on the leeches of Japan (1886) Whitman records some very interesting observations on the behavior of the land leech under varying internal and external conditions, and it is rather remarkable that these seem to have escaped the attention of the workers on annelid behavior. A later contribution (1891) enters rather fully into the breeding behavior of leeches in general, but particularly in relation to *Clepsine plana.* In connection with this, he includes a rather full discussion of the literature bearing on this type of reactions. With the exception of one paper by Von Uexküll (1905), the most extensive single contribution to leech behavior is Whitman's lecture on Animal Behavior (1898), in which he considers rather fully the sensitivity and deceptive quiet reactions of *Clepsine.* Certain of his facts and conclusions related to this work are quoted in connection with the special topic to which they apply.

Verrill (1872–1873) has presented an extensive systematic account of our North American fresh-water leeches, but says little in regard to general habits. In discussing the relation of the Hirudinea to fisheries he writes the following: "The leeches are related to the fisheries in three ways. Some of the large blood-sucking species like *Macrobdella decora* and the species of *Hirudo* attack many fishes directly, even when of considerable size, and destroy them very quickly by sucking their blood; and the species of *Icthyobdella* and *Cystobranchus* are true parasites of fishes, and, often when numerous, do them much injury. Other kinds like the various species of *Clepsine, Nephelis, Aulastomum*, etc., destroy all sorts of small mollusks and worms, which otherwise might become the food of fishes. But, on the other hand, certain kinds of leeches are fed upon to some extent by the lake whitefish and probably by other fishes."

Apathy (1888) devotes considerable space to the description of the locomotor movements of the various genera of leeches. These are so distinctive in type in the various forms that he feels warranted in the statement that "in der verschiedenen Art und Weise der Locomotion sehe ich nämlich einen wichtigen Fingerzeig für die Phylogenie."

Loeb (1894) in his work on the brain physiology of the annelids discusses briefly the righting movements and general reactions of decapitated leeches.

Beddard (1896) brings together what is known in regard to leeches generally. Particular consideration is given to classification and morphology, relatively little attention being given to the general reactions of leeches.

Gibbs (1897–1899) in a very interesting note states that the skate-leech *Pontobdella muricata* incubates its eggs. A female of this species was secured mounting guard over a group of eggs attached to the flat valve of a scallop shell, *Pecten maximus*. The incubation period of this individual occupied at least 123 days. Of this behavior Gibbs says: "For what purpose the skate-leech remains with its eggs during incubation appears uncertain. One may presume that their protection is the chief object; whether from active enemies or from the mere accumulation of sand, etc., is doubtful."

Bristol (1898) in connection with his work on the metamerism of *Nephelis* includes a few notes on his experience in collecting and keeping leeches which he used in his dissections.

Graf (1899) in his splendid "Hirudineenstudien" considers, from a comparative point of view principally, the structure and function of the nephridial system of leeches. To a certain extent, also, other features are included, and incidentally some remarks with regard to the feeding reactions of *Nephelis*.

Brumpt (1901) treats at considerable length the question of reproduction in the *Hirudinea*. The structure of the reproductive organs in the various groups of leeches is discussed, as are also the questions of spermatogenesis, ovogenesis, and fertilization. The breeding reactions of several genera are also given.

Holmes (1905) in his paper on "Random Movements" discusses the general features of phototaxis in *Glossiphonia*. Some of his comments are as follows: "The method of orientation in these forms is in principle the same as that of the earthworm. When specimens of *Glossiphonia* are placed in strong light their locomotor reflexes are set in action. In its progress the leech frequently raises the extended anterior part of the body and waves it from side to side as if feeling its way. If the animal turns it in the direction of the strong light it is quickly withdrawn and extended again, usually in another direction. When the leech becomes negatively oriented it may crawl away from the light, like the earthworm, in a nearly straight line. Of a number of random movements in all directions only those are followed up which bring the animal out of the undesirable situation."

Von Uexküll (1905) has explained in a very original and suggestive way and with considerable detail "das Schwimmen," "Verkurzung und Sperrung," "das Gehen," and "Schleifenreflex und Umdrehreflex" in the blood-leech. This is by far the most extensive piece of recent work bearing on the behavior of leeches. It considers, however, principally the physiology of the locomotor movements of the blood-leech. The general reactions, such as feeding, responses to contact, light, etc., and the modifications of these, are not included in his study. His views in regard to the locomotor movements are considered in the discussion of those responses in a succeeding portion of this paper.

Bohn (1907) has provided us with a more recent contribution than that of Von Uexküll. This appeared in the form of a short paper discussing the relation of tropisms, differential sensibility, and associations in the behavior of *Branchellion*, a leech parasitic on the torpedo. This *Branchellion* he records as being very strongly positive to light, the intensity of the light determining the degree of random movements previous to orientation. He finds it possible to change the character of the phototactic responses by lack of salt in the water, decapitation, and prolonged insolation or exposure to the sun. In order to explain certain of the reactions of this form, he makes use of "*phenomenes associatifs*" of a simple type.

Masterman (1908) discusses the *Hirudinea* as human parasites in Palestine. Portions of his paper are of such a significant nature as to warrant quoting in their entirety. "Leeches are common in the fountains and pools of Palestine, particularly in the northern parts known to us familiarly as 'Galilee' and farther north in the district of Lebanon. In the later summer and autumn months they are so plentiful in places that almost every horse and mule passing through these parts has a bleeding mouth. Under such conditions it is not wonderful that human beings from time to time are attacked. . . . Many of the springs in the mountains of Galilee and in Lebanon are widely known for the multitude of leeches which lurk in their waters, but a thirsty traveler seldom has self-control to restrain himself from drinking, and when he does so, particularly at dusk or in the night, he is very likely to suck one in! . . .

"In the cases, some three dozen or so, which I have had under my own observation, the leech has been attached to the epiglottis, the pharynx, the nasal cavities, or, most common of all, the larynx. . . . The haemorrhage, though never great in quantity at any one time, may, when prolonged, be very serious and even fatal. I know of two cases where the patient has actually died from this." The species he gives as *Limnatis nilotica*.

Harding (1910) in a paper on the British Leeches, which is primarily a systematic account, includes the habitats and foods, so far as known, of a number of the species.

Biedermann (1910) in Winterstein's *Vergleichende Physiologie* discusses rather fully the literature bearing on the food-taking and digestive processes in the Hirudinea.

Moltschanov (1911) records *Hemiclepsis marginata, H. tessulata, Glossiphonia heteroclita,* and *Gl. bioculata* as carrying their eggs attached to the ventral surface of the body. Upon emerging from the egg, the young leeches attach themselves by their suckers to much the same ventral portion of the parent as was occupied by the eggs and remain in this position until about one-third grown. The epithelial cells are specially modified so as to provide the easy attachment of the suckers, and it is suggested that the secretion of these cells furnishes food material for the young leeches.

Bolsius (1911) confirms in large part the observations of Moltschanov, and places *Glossiphonia sexoculata* among the species which carry their young. This species he records as carrying about fifty young per individual; while in *Hemiclepsis marginata* he states that he has seen as many as ninety-two young inflicting themselves upon a single adult.

Nachtrieb, Moore, and Hemingway (1912) in their discussion of the leeches of Minnesota give much interesting material on the structure and classification of leeches, with a brief treatment of the natural history of these animals. Moore includes in his classification observations on the food of *Glossiphonia stagnalis* and *Hemiclepsis occidentalis.* An excellent description of this latter form is also included.

III. DESCRIPTION OF MATERIAL

The experiments described in the following pages were confined exclusively to three species of leeches, each representative of a different genus. The great bulk of the results was secured from the nephelid *Dina microstoma* Moore and from *Glossiphonia stagnalis* Linnaeus. Specimens of *Hemiclepsis occidentalis* Verrill were more difficult to secure and for that reason form the basis for relatively few observations.

Dina microstoma is fully described by Moore (1901) in his paper on "The Hirudinea of Illinois." The species is generally slender, and approximately 42 mm. in length. The mouth is

small even in specimens killed in a relaxed condition. The recorded range of this species is, so far as I have been able to discover it, Ohio, Illinois, Pennsylvania, and California. The material used in the following experiments was secured in Fruitvale, California, from a fresh-water pond among the foothills of the Coast Range Mountains. The pond even during the rainy season is only a few feet in depth and in the autumn months becomes reduced to only a few inches. It is liberally supplied with various aquatic plants, and is provided with a most copious bottom of black mud. By dredging this mud from the bottom of the pond the leeches were secured in great abundance. No difficulty whatever was experienced in keeping them alive and in good condition for months in the laboratory. They were placed in aquaria containing a few inches of water, a few algae, and *Ceratophyllum,* and a stone for a hiding place.

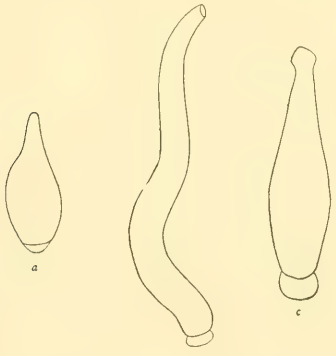


Fig. 1.—Outline drawings of leeches studied, showing relative shapes and sizes. (*a*) *Glossiphonia stagnalis* Linnaeus, (*b*) *Dina microstoma* Moore, and (*c*) *Hemiclepsis occidentalis* Verrill.

By far the most abundant leech that I have been able to discover in this locality is *Glossiphonia stagnalis* Linnaeus. The best description of this species is that by Castle (1900). The leech is a relatively small one, approximately 8–10 mm. in length

and 5 mm. in width. It is an exceedingly active species, and very extensile, the body when extended being ten times as long as broad. It is found in Europe, the adjacent parts of Asia and Africa, and in North and South America. The material secured in connection with the work in this paper was obtained from an artificial lake in Golden Gate Park, San Francisco. The specimens were found clustered by the hundreds underneath the stones along the margin of Stow Lake. When brought into the laboratory they are rather more difficult to keep alive than are the *Dina* above mentioned. The water must be frequently changed, and the animals fed more often than in the case of the *Dina*. Earthworms provided the best food material, especially since these are readily procured and the leeches feed voraciously upon them. As compared with other living material, I have found leeches remarkably easy to keep for long periods in good condition. For this reason they provide an exceptionally favorable material for experimentation.

IV. CATEGORIES OF MOVEMENTS IN LEECHES

1. Basis for Classification

The repertoire of movements in the leech is not a very extensive one, though the different responses show a wide range of modifiability in both vigor and duration. These reactions may be classed as the random side-to-side (lateral) and up-and-down (vertical) movements the crawling or "looping" reaction, the "swimming" response, the undulatory respiratory movements, the feeding responses, and the breeding reactions. The general features of all of these categories of responses have been studied, with the exception of the behavior during the breeding season. Unfortunately, the material for the nephelid studied showed no tendency toward breeding, though kept in the laboratory through a period of several months. In the case of the species of *Glossiphonia* and *Hemiclepsis* used in this study, specimens were found carrying their eggs and also their young. This fact afforded the opportunity for the study of the *possibilities* of the presence of a rudimentary "parental instinct."

2. Random Movements

Too much stress cannot be placed upon the part played by random movements in the behavior of the leech. Its life is one of repeated trial, and the adaptiveness of its selective action from among the many varying factors of its environment usually serves to steer the animal effectively out of regions unfavorable to its continued existence, and into proper environmental conditions.

These random movements are effected mainly by the action of the dorsi-ventral and lateral longitudinal muscles of the body, the circular muscles performing a more or less accessory function. The movements, depending largely upon the strength of the evoking stimulus and the physiological condition of the organism, may vary from a slight, slow vertical or lateral turn to a complete and rapid turn to the right or left, resulting in an entire reversal of direction of movement in the animal. Upon the animal's coming into an unfavorable environment, such as an area of superoptimum light-intensity, the number of random movements is very much increased, with the final result that it becomes oriented and moves away in a direction opposite to the source of light. This in its normal habitat would serve in most cases to remove the leech into a region more nearly its optimum of light-intensity. Chemical stimuli, favorable or unfavorable, serve to intensify the random responses: the one being followed up, the other usually successfully avoided through many trials. Higher temperatures than normal and increased sensitivity resulting from mechanical stimuli such as contact or jars produce the same general effect.

Nor is it necessary, particularly in the case of the nephelid, for some stimulus to be applied to observe this tendency to random movements. Almost every looping response of the animal in its progress forward is preceded by a series of random movements of the anterior end. So thorough is the exploration of the advance ground, at times, that the body of the animal describes several very wide arcs of a circle before orientation is finally effected. This tendency to "prove all things, hold fast that which is good" is perhaps the most striking single characteristic of the behavior of leeches, and undoubtedly, due to the flexible nature of the response, serves a most important adaptive purpose in the life of the animal.

3. Looping Response

The looping reaction is so designated on account of its resemblance to the movements of the Geometrid larvae or "measuring" worms. Von Uexküll (1905) describes this type of response in the blood-leech as "das Gehen," preferring this term to "Kriechen," because not all of the ventral surface of the animal is in contact with the substratum, the suckers of the animal being the parts of the body on which most pull is exerted.

The circular muscles contracting antero-posteriorly, and the longitudinal muscles extending, the anterior end of the animal is pushed forward, the arch produced in the preceding crawling movement serving as a leverage to assist the muscular action more easily to push forward the anterior portions of the body. Executing random movements and becoming oriented, the anterior end of the body, which serves as the anterior sucker, is applied to the substratum. Antero-posterior contraction of the longitudinal muscles now takes place, more rapidly than did their extension, and in the nephelid the posterior sucker is drawn along in contact with the surface without its being lifted from the substratum. The posterior sucker is advanced only a portion of the distance between its place of attachment and that of the

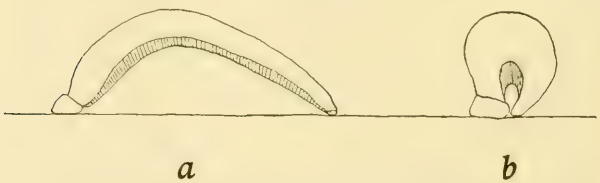


Fig. 2.—Looping responses: (*a*) of *Dina microstoma;* (*b*) of *Glossiphonia stagnalis.*

anterior sucker in the case of *Dina microstoma;* in *Glossiphonia* and *Hemiclepsis* it is usually placed closely against the anterior. This difference is indicated in the accompanying figure (fig. 2, *a, b*). In the latter two genera, with each loop, in many cases, the posterior sucker is released from the substratum and placed near the anterior, differing in this respect from the movements of the nephelid. In *Glossiphonia,* however, the posterior sucker

frequently remains in contact with the substratum, and is dragged along as in the case of *Dina*. In *Dina*, stronger stimulation may produce lifting of the sucker of this region, but the leech does not seem to be able again to attach this quickly enough to complete the looping movement within the normal length of time. This is perhaps to be explained as due to the flattened shape of the body produced as the result of the contact stimulation, this expanded condition preventing the posterior sucker from readily attaching itself. Upon the attachment of the posterior sucker, the anterior end is released and the movement as described above again performed. These looping responses, following each other in rapid sequence, serve to carry the animal forward with a fair rate of progression.

4. Swimming Response

This is provoked rather easily upon stimulating the posterior end of the animal, the strength of the stimulus governing to a great extent the vigor of the response. It is also secured upon rather strong stimulation of the anterior end, usually under these conditions, following a complete recoil and consequently a complete change of the direction of the movement of the leech. The reaction consists in a rhythmical undulatory muscular contraction proceeding antero-posteriorly. The body strikes up and down in the water, or the lateral axis of the body may become vertical in position, and the body of the animal be lashed from side to side. A very characteristic feature of this "eel-fashion" of swimming is the dorsi-ventral flattening of the body. This serves to reduce the resistance in movement through the water, and at the same time affords a greater propelling surface with which to drive the animal forward.

To a stronger stimulation of the posterior end the animal responds with more rapid undulatory movements of the entire body, the lateral axis of the body becoming vertical instead of retaining the normal horizontal position. Greatest speed seems to be secured in this way. To the average stimulus, more often, the normal dorsi-ventral position is assumed; and while the undulations of the wavelike course of the animal are less deep

in the more rapid movements, yet the same whiplike motion carries the body forward.

Cessation of movement in the swimming reflex takes place by a slowing up of the rhythmical movements, followed by attachment of either the anterior or posterior sucker first, the other one becoming attached immediately afterwards. In one individual twenty-four swimming reactions were observed in order to see which sucker was most often attached first. The following are the results: Anterior sucker attached first, 19 times; posterior sucker attached first, 5 times. This is to be explained by the fact that the anterior end, being foremost in locomotion, most often comes first in contact with the surface upon which the animal comes to rest, or to attach itself and take up the looping type of locomotion.

In the species of *Glossiphonia* and *Hemiclepsis* studied, the swimming reaction was not observed at all, no amount of stimulation being successful in evoking this type of response. Both of these species carry their young attached to the ventral surface of their bodies. A special modification of structure accompanies this mode of behavior, the body being so shaped as to form a pouch-like cavity underneath the ventral surface, and it is evidently due to this difference in structure that we have this corresponding difference in behavior. Von Uexküll (1905) has described the swimming movements in the blood-leech. Both the blood-leech and the nephelids do not carry their young, but form cocoons, much as the earthworm does. Thus it seems probable from the forms studied that those groups of leeches which carry their young are so modified thereby in structure as to be rendered incapable of the swimming reflexes, while those that are not encumbered with such a burden are provided with this freer and more rapid mode of locomotion.

5. Undulatory Respiratory Movements

When allowed to remain undisturbed in the aquaria for some time, many of the leeches fix themselves by the posterior sucker and exercise undulatory movements of the body. These are much the same as the swimming movements already described,

with the necessary differences that they are much more slowly executed and no progress forward is made as a result of them. The body is not so flattened as in the swimming movements and sways frequently from side to side. In *Glossiphonia stagnalis* the undulations are necessarily not so pronounced as in *Dina*, owing to the differences in structure of the body in the two genera. However, the execution of undulatory movements is to be observed as frequently in this species as in the nephelid.

These movements were observed by Moquin-Tandon (1846), who says in regard to them: "Plusieurs *Hirudinées*, telles que les *sangsues*, les *Néphélis*, la plupart des *Glossiphonies*, aiment beaucoup à se fixer par la ventouse anale et à se balancer dans l'eau. . . . Les *Néphélis* par un balancement ondulatoire, mettent leur peau en contact incessament renouvelé avec l'air dissous dans l'eau. Les *sangsues* et les *Haemopsis* exercent plus rarement les mouvements dont il s'agit mais ces animaux sont moins exclusivement aquatiques que les *Néphélis*. Les *Glossiphonies*, qui ne peuvent pas vivre hors de l'eau, nous offrent des espèces qui se balancent avec vivacité, et d'autres qui restent presque constamment immobiles; mais ces dernières viennent souvent à la surface du liquide où elles se tiennent le corps moitié dans l'air, moitié dans l'eau."

As already mentioned, during these movements the body sways from side to side, as if exploring in a limited way the immediately surrounding region of its environment. It was conjectured that perhaps the movements were connected with the feeding reactions, enabling the leech more readily to locate the food about it. So the effect of the addition of some extract from a couple of macerated snails (*Limnea*) was observed in order to determine whether the undulations might not be readily evoked in this way. Six small dishes, each containing two specimens of *Dina* and kept quiet for a couple of hours previous, were used, the last being kept for a control. Though strengths varying from one to ten drops in the separate dishes were used, no responses of the nature of undulatory movements was evoked in any of the dishes, the diffusing juices of the macerated snail serving only to excite the animals to more vigorous locomotor movements.

The natural assumption, and that suggested by Moquin-Tandon (1846) in the above quotation, is that these undulatory movements serve a respiratory function. Several dishes of *Dina*, fed three days before, and hence in a normal condition, were supplied with stagnant and to a certain extent putrid water from a jar in the laboratory. Controls were used, supplied with tap water. Within an hour all of the individuals in the foul water either had been, or were, exercising undulatory movements, while many of those in the dishes of tap water were quiet on the bottom of the dishes, none of them having exercised undulatory movements. Foul water is not alone characterized by low oxygen content, but by decomposition products as well. So a similar series of experiments was conducted, using boiled water instead of foul water. The same results were secured. After the animals had been in the water for some time it was observed that their general tonus became lowered as the result of the interference of the low oxygen content of the water with the normal processes of the organism. As a consequence of this condition, the animals showed more sluggish tendencies, remaining quiet much more than was the case with the normal individuals in the control dishes.

These experiments indicate that the movements have a respiratory function, together, perhaps, with that of excretion, enabling the nephridia more easily to discharge their excreted substances to the exterior. An accessory function without doubt is the removal of accumulating debris from the surface of the body. In jars, where the material of this kind was loosened from plants in removing specimens for experiments, it was observed that the falling fragments were oftentimes the means of inducing these movements which very effectively remove the debris from the body.

It is interesting to note that the undulatory movements were observed to take place in a piece of only a few millimeters in length, cut from the middle region of the body.

6. Righting Reactions

The position in which the body of a nephelid comes in contact with the surface of the dish determines very largely the nature of the righting response. If the body is arched, as is often the

case, when dropping through the water, and approximately the mid-dorsal surface comes in contact with the bottom of the dish, the response is a muscular movement, straightening the body and turning it towards the side on which the center of gravity happens to lie. Either the anterior or posterior sucker may be attached first, the body then being twisted over into its proper position.

The righting process is usually accomplished with the aid of the suckers. Sometimes, however, it may be performed by the swimming reaction being given, the specimen orienting its body properly by the steering action of the anterior end. Loeb (1894) noted in regard to the righting reaction of blood-leeches which had been operated upon: "Legt man das hintere Stück auf den Rücken, so beginnt es Schwimmbewegungen zu machen, durch welche es sich in die Bauchlage zurückbringt. Das vordere Stück erreicht die Bauchlage durch direktes Umwenden." In the species of *Dina,* where the posterior three-quarters of the body has been removed, the righting is, as Loeb has described it for the blood-leech, by a direct turning. The anterior sucker is attached and the body turns toward the side on which the center of gravity happens to fall. In the posterior portion, when the anterior sucker has been removed, the responses to reversed position of the body may be swimming, and the righting may take place during this process. Often, however, the response is a direct turn, as in the anterior portion. The posterior sucker inclines toward the substratum, becomes attached, and turns the animal, aided by the leverage derived from the pressure of the anterior end against the bottom of the dish. Even a section a few millimeters in length removed from the middle region of the body will right itself through a contraction of the dorsi-ventral muscle exerting a pull toward the ventral side and thus turning the body over to its normal position.

The righting reaction in *Glossiphonia* is more stereotyped than in *Dina microstoma.* It is usually accomplished by the attachment of the anterior sucker and a twisting pull is exerted, much as Pearl (1903) has described in the planarian, by means of which the body is turned into its proper position. The posterior sucker is brought close to the anterior and the leech loops forward.

V. GENERAL RESPONSES TO STIMULI

1. Formation of Collections

Often in the aquaria the nephelid leeches may be seen in twisted masses, their posterior ends attached, but usually the anterior suckers free. This is particularly noticeable when no large solid object, such as a stone, is present for them to crawl under and satisfy their stereotropic propensities.

Smith (1902), working on *Allolobophora foetida*, finds: "If a number of worms are put down near each other they soon crawl together and coil into a heap. . . . It is a common observation that earthworms have the habit of lying coiled together in masses. Darwin refers to this habit of *Lumbricus* in his 'Formation of Vegetable Mould,' and Hofmeister (1845) says earthworms pass the winter, either singly or rolled up with others, at the bottom of their burrows." Pearl (1903) has recorded the formation of collections in planarians in the angles of the dish in which they may be kept in the laboratory. Riley (1912) observed in the dragon-fly nymphs a very pronounced tendency towards the formation of groups, and a similar condition has been described by the Severins (1911) for some of the aquatic Hemiptera.

In order to determine what effect a lowering of temperature might have on this formation of collections, a dozen leeches were placed in a crystallization dish in a tightly closed icebox at a temperature of about 10° C. A control was operated on top of this, lighted by a practically uniform illumination from a skylight above. This was continued for a couple of days, and a more manifest tendency towards the formation of collections was observed in the control than in the dish in the refrigerator. The chief influence of the cold seemed to be that of lowering the vitality of the animal and causing it to remain quiet for the greater part of the time. Thus temperature differences uniform throughout the dish seem a negligible factor in producing these collections, which is perhaps to be explained by the fact that the body of so lowly organized an animal as the leech very quickly takes on the temperature of the surrounding medium.

Examination of the position of these collections usually reveals that they are located in the least lighted portions of the dish. In the center of many of them can be seen a mass of debris, which, coming in contact with the body of the first one or two leeches forming the group, causes a cessation of movement. The others composing the collection were directed to the same locality by the influence of the light rays and came to rest one by one until a considerable group was established. As already suggested, the animals show a very strongly positive thigmotaxis. Undoubtedly, optimum light conditions and thigmotactic responses are the chief factors operative in the formation of collections.

This tendency to formation of collections is much more manifest in *Glossiphonia stagnalis* than in *Dina*. Even under stones in their native environment large groups are to be found. When the groups are formed in dishes in the laboratory they occur principally in the angles of the dish. Often as many as fifty to a hundred individuals are to be found composing a single collection.

2. Food of Leeches

Moquin-Tandon (1846) has observed: "Les *Néphélis* mangent des *Limnés* et des *Planorbes;* elles s'emparent aussi des *Planaires,* des *Monocles,* des petites larves aquatiques et des animalcules infusiores. Il parait d'après la structure de leur bouche, qu'elles ne se contentent pas de sucer ces animaux, mais qu'elles en avalent des portions considérables." Of *Herpodella otoculata,* a form related to *Dina microstoma,* Harding (1910) says: "This and the succeeding species devour small oligochaetes such as *Tubifex,* planarians, and probably a variety of other soft-bodied animals." Bristol (1898) in his work on the metamerism of *Nephelis* records the fact that he "fed chopped freshwater clams. . . . I have kept individuals for over a year in normal condition, and have raised many young under these conditions." Iijima (1882) in his paper on the embryology of *Nephelis* says: "If well fed with fish meat or larvae of mosquitos, *Nephelis* will lay eggs in abundance."

Thus it is to be observed that the recorded range of food materials for nephelids is wide. I have kept snails (*Limnea, Planorbis,* and *Physa*) and *Dina microstoma* in aquaria together for weeks, but have yet to see the leeches attack a living snail. Often they are to be seen twisting themselves around the snail, but always, sooner or later, the snail successfully rids itself of them. When a gash was cut into the foot of the snail with a scalpel they were observed to feed on the injured part until the snail withdrew into its shell. However, they fed vigorously upon crushed snail. A young living earthworm was placed in the dish with several *Dina*, with the result that it was lacerated to death through the sucking action of the leeches and finally completely eaten, a fragment at a time. Older earthworms met with a similar though not so rapid and complete destruction. A recently dead crayfish, with its body severed in two, was fed to the voracious animals, which attacked it with as evident relish as they later fed upon a freshly killed minnow cut in pieces, and also one dead for a couple of days. A dead salamander was fed to some hungry individuals and, while not vigorously fed upon, yet it was partaken of by several of the leeches. The same held true in the case of a *Belostoma* which had been dead for a day or two. Thus the food of this species of leech serves to point towards its being to a large extent a scavenger.

Castle (1900) says of the leeches of the family Rhynchobdellidae to which the genus *Glossiphonia* belongs: "The smaller species feed upon snails, crustacea or other small fresh-water animals." Harding (1910) states in regard to *Glossiphonia complanata:* "It is parasitic chiefly upon *Limnea* and *Planorbis,* but also attacks other fresh-water mollusks, the larvae of *Chironomus* and probably aquatic annelids." It was found possible to keep *G. stagnalis* in good condition for weeks by feeding them earthworms, from which they sucked the blood. No feeding experiments were conducted upon *Hemiclepsis occidentalis.* Of a related form, *Hemiclepsis marginata,* Harding says: "This species is a fish parasite. Apathy states that it attacks the smaller species of carp."

3. Feeding Reactions

Upon the addition of a few drops of freshly macerated snail juice to the water in a dish containing a number of *Dina microstoma* these leeches are stimulated to greater activity. Rapid, short-distance swimming reactions are given, the animals settling quickly to the bottom of the dish, executing random feeling movements, and, if successful, again swimming off or crawling rapidly about in the dish. If while the animal is attached and crawling a slight stimulus is applied by drawing a glass capillary rod up alongside of the anterior end, it reacts usually towards it, applying the anterior sucker to the glass rod, and then quickly withdrawing it. In many cases the anterior tip of the body is coiled around the rod, and the anterior end applied to it, followed by a recoil. Though momentary, it is yet a decided positive reaction. This type of response is secured from contact stimulus alone, as is discussed in a later portion of this work. However, it is accentuated under the influence of diffusing food juices, as well as by a starved condition of the leech.

The food is located by "trial and error" movements, and is often crawled over and under by the leeches without its presence serving to check all of them. When the anterior sucker comes in contact with the soft body of the snail there seems to be a reinforcing stimulus to the contact response set up by the concentrated snail juice, and the animal holds on literally as well as figuratively "for dear life." This constitutes the difference between the response merely to contact under the influence of diffuse snail juice, since there, due to the weakness of the food juices, contact is not reinforced sufficiently to be followed up by the feeding reaction.

Whitman (1886) observed in one of the blood-leeches the following: "A drop of fresh blood was allowed to flow from a pipette over the dorsal surface of a leech while in a state of repose. The leech kept up a gentle undulatory movement of the body and gave no evidence of recognition. As soon, however, as the blood flowed over the margin of the lip the leech became aware of its presence." In *Dina* the application of macerated snail juice was found to be effective only in producing greater

activity, or positiveness of response, when made at the anterior end, or when the diffusing food juices had come in contact with the mouth region of the body. This is very closely in accord with what has been found by Whitman in the blood-leech, and from such behavior one is inclined to conclude that cells adapted to taste functions are present principally in the mouth region of the leech. This view is further strengthened by the fact that diffusing food juices have practically no effect upon decapitated specimens.

The family to which *Dina microstoma* belongs is characterized as "non-parasitic, carnivorous, and without denticulate jaws." In *Glossiphonia stagnalis* the position of the mouth, according to Castle (1900), is in the third somite, and leads dorsally into the pharyngeal sac, which continues backwards, ending in the thirteenth somite. A short oesophagus, extending the length of only one somite, connects this with the crop.

In the feeding of *Dina microstoma,* the posterior sucker is attached either to the bottom of the dish or to the surface of the material on which the animal is feeding, and the anterior sucker is applied to the food. The feeding seems to be a combination of sucking and tearing; the mouth is applied for many seconds continuously and then suddenly the head may be pulled loose from the mass of food, and later reapplied. The animal seems to have the power as described by Moquin-Tandon of removing often considerable pieces of food and swallowing them entire. The appearance of a worm or a piece of snail after the animal has fed to satiety is another very good piece of evidence to substantiate such a view, since there is little or none of it left.

Whitman (1898) says: "Many species of *Clepsine* require but one full meal a year, and as they seldom live more than two or three years the number of meals is very limited." Starvation experiments conducted on *Dina microstoma* show that after more than six months of fasting eight specimens of this species still retain considerable vigor. There is evident in these specimens, however, a marked reduction in size.

When a dish containing a number of active *Glossiphonia* is provided with a couple of earthworms, only a few minutes suffice for the most of the leeches to locate the prey. Of certain species

of *Clepsine* (*Glossiphonia*) Whitman (1898) says: "They probably recognize their right host by the aid of organs of taste; at any rate, they are often able to distinguish their host from closely allied species." *Glossiphonia stagnalis* assumes a very characteristic feeding position, similar to that of the last stage of the looping reaction. The posterior sucker is fixed close to the place of attachment of the mouth, and rhythmical muscular movements pass antero-posteriorly over the body. This sucking action must serve to rupture the epidermal tissues of the earthworm, since this species of leech does not possess denticulate jaws. The hold is scarcely loosed until the leech has completely gorged its digestive tract. The outline of this stands out plainly through the partially transparent cells of the body wall. When in this condition of mechanical fullness the animal releases its hold on the unfortunate victim, and moving away soon comes to rest in the society of its fellow-leeches, which perchance are already undergoing the wholesome effects of a bloody meal.

4. Sensitivity to Various Stimuli

Whitman (1898) has pointed out from some of his experiments the extreme sensitivity of *Clepsine*. He placed leeches of this genus in a shallow, flat-bottomed dish and allowed them time to become acclimated. "Then taking the utmost care not to jar the dish or breathe upon the surface of the water, look at *Clepsine* through a low magnifying lens and see what happens when the surface of the water is touched with the point of a needle held vertically above the animal's back. If the experiment is properly carried out, it will be seen that the respiratory undulations (if such movements happen to be going on) suddenly cease and the animal slightly expands its body and hugs the glass. Wait a few moments until the animal, recovering from its normal composure, again resumes its respiratory movements. Then let a needle descend through the water until the point rests on the bottom of the dish at a little distance from the edge of the body. Again the movements will cease and the animal will hug the glass with its body somewhat expanded. Now push the needle slowly along towards the leech and as the needle comes almost

in contact with the thin margin of the body that part nearest the needle begins to retreat slowly before it. This behavior shows a surprising keenness of tactile sensibility, the least touch of the water with a needle point being felt at once."

These experiments of Whitman were repeated on a couple of specimens of *Hemiclepsis occidentalis* with the same striking results recorded in his paper. Upon puncturing the surface film the animal was observed to hug the bottom of the dish, remaining quiet for a considerable length of time, often more than ten minutes. Pricking the surface of the animal would produce only a local contraction of the part stimulated without any general movement of the body. The reaction is, as Whitman suggests, very similar to that of the death feint in the higher invertebrates. Passing the hand over the dish will cause an active *Hemiclepsis* to elevate the anterior end and exercise feeling movements about in the water. The positive reaction to a shadow seems to be absent in *Dina,* though a decided negative response is secured to even very slight shadows cast over the dish. This is particularly noticeable when the leeches are executing the undulatory respiratory movements.

The deceptive quiet of *Dina microstoma* is very much less marked than in the *Hemiclepsis* above mentioned. Animals placed in a circular glass dish 12 cm. in diameter and containing water to a depth of 2 cm. were allowed to remain in a room with rather dim, diffuse daylight without the slightest jar for four hours and were in a slowly active condition. Then a glass rod was applied to the surface film. In some cases the animal stopped immediately and hugged the bottom of the dish for several seconds. Again, little response was secured from some of the individuals, these continuing their forward movements, entirely disregarding the slight stimulus. An interval of fifteen to eighteen hours of absolute quiet made the animal much more responsive to the slight stimulus, a much larger per cent showing the deceptive quiet reaction. The duration of this is, however, very much less than in *Hemiclepsis.* Contact stimulation of the animal when in this condition of quiet, even of very slight intensity, produces a marked negative reaction, a condition quite different from that obtained in *Hemiclepsis.*

In the experiments on *Dina,* the capillary rod was pushed to the bottom of the dish, while the animal was displaying the deceptive quiet reaction, about an inch from the anterior end of the leech, and moved slowly towards it. When the rod came close to the body the animal responded by turning towards it, immediately recoiling upon contact. Even to this slight stimulus, if repeated similarly, the animal will often reverse the direction of its movement by a sharp turn.

Place a number of individuals attached to the under surface of a stone in an aquarium near a window and allow them to remain undisturbed for some time. The anterior third to half of the body will be extended from underneath the stone, and undulatory respiratory movements executed. If some dark object, such as a large piece of cardboard, be interposed between them and the window, the undulatory movements will immediately cease, the animal hugging the bottom of the dish. Allow this to remain, or remove it, as you like, and in many cases the animal will quietly resume its undulatory movements. To a very slight jar of the table or dish the same type of response is given as to the shadow. The leech is an extremely sensitive animal, and, as pointed out by Whitman (1898), unless considerable care is exercised, oftentimes, the experimenter is likely to overlook this fact, since the leech is also an animal capable of withstanding conditions involving severe tests of vigor, as will be shown in a succeeding portion of this paper.

5. Reactions to Light

The leeches studied were found to show a marked negative phototaxis. Upon their being brought into the laboratory and placed in a long glass dish facing the window it was a matter of only a few minutes before the major portion of them had made their way to the less illuminated part of the dish. A similar reaction was secured in response to the stimuli of a 60-watt and of a 100-watt Mazda electric lamp. It has been mentioned elsewhere that both *Dina microstoma* and *Glossiphonia stagnalis* are nocturnal in habit. When allowed a stone in the aquarium for a hiding place, these leeches are content to remain underneath it during the day.

Random movements play a considerable rôle in the responses of the leech to light. Tests made on *Glossiphonia* indicate that the higher the degree of illumination the greater the initial excess of random movements. This fact is apparent upon comparing the accompanying diagrams (figs. 3, 4). These were secured by placing upon a rigid glass plate a flat glass dish containing the leech to be tested. The leech was placed in each case directly oriented toward the source of light, and this was then turned on. With a sharply pointed wax pencil the course of the leech was traced on the glass underneath the leech itself as it moved forward. From this glass plate a copy of the route pursued by the leech was taken. Out of many surplus movements, the leech follows up only those that tend to rid it of the stimulating agent. Orientation of the body of the leech so that its two sides are equally stimulated by the light occurs, however, in only a relatively few cases.

Fig. 3.—Influence of 100-watt Mazda light on the direction of movement of five leeches of the species *Glossiphonia stagnalis;* (*e*) representing the responses of an individual which left the bottom of the dish for the surface film.

The amount of direct turning in the responses of *Dina microstoma* was tested in the following manner: A well-moistened piece of filter paper was placed on a glass plate in turn resting upon a flat revolving disk. The leech was removed from the aquarium and placed upon this piece of filter paper. The animal was allowed sufficient time for its body to become straightened out in forward movement. The disk was then turned so that the body length was at right angles to the source of light, a 60-watt Mazda. These operations were performed by the aid of the red light in a dark room, and when the body of the animal had been properly oriented for the experiment the light was turned on. The first turn of the body was carefully noted and the light immediately turned off again. In the accompanying table the turns toward the source of light are recorded as positive (+) and those away from the light as negative (—). The indifferent responses are those cases where the leech continued its forward movement. However, the stimulus of the light was allowed to continue acting on these cases until the leech had turned either towards or away from the source of illumination.

TABLE I

DIRECTIVE INFLUENCE OF 60-WATT MAZDA LIGHT ON *Dina microstoma*

Light falling on right side of the leech

	Number of the leech					
	1	2	3	4	5	6
Towards (+)	9	6	10	5	7	4
Away (—)	9	9	11	14	11	8
Indifferent, followed by (+)	1	3	1	3	3	5
Indifferent, followed by (—)	6	7	3	3	4	8

Light falling on left side of the leech

	Number of the leech					
	1	2	3	4	5	6
Towards (+)	6	7	5	4	8	2
Away (—)	10	16	15	15	11	15
Indifferent, followed by (+)	3	0	1	4	0	3
Indifferent, followed by (—)	6	2	4	2	6	5

None of the turns, except in a few cases, was so abrupt as to cause a direct reversal of the direction of movement in the leech. The light of the intensity used does not produce so powerful an effect. The turns were comparatively slight, though

well defined. In these experiments the entire body was illuminated on the side toward the light. Under such conditions, as can be noted from the accompanying table, there is a decided excess of turns away from the source of light. Continued illumination produces, in the cases where the first response is indifferent, usually a turn away from the source of light.

The accompanying diagrams (figs. 3, 4) represent the paths pursued by several *Glossiphonia* in their movement away from the light. A study of these will indicate the part played by direct turns in their orientation. Although the initial excess of random movements under the influence of a 100-watt Mazda light is greater than that caused by a 25-watt light, there is a decided difference in the orientation effected. As the leech moves farther away from the 25-watt light the number of random movements becomes much increased. When orientation is effected as the result of the 100-watt light it continues with little random movement across the remaining length of the 25 cm. dish.

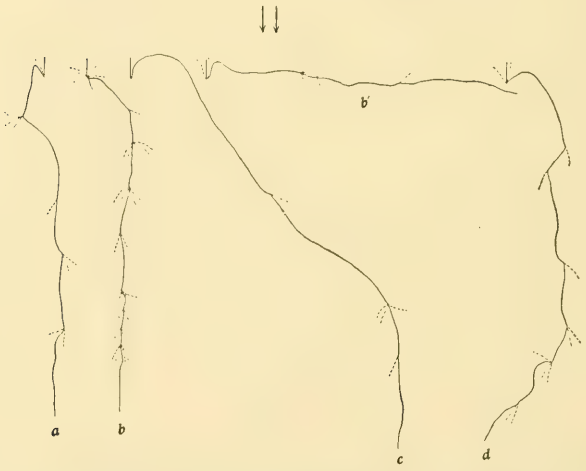


Fig. 4.—Influence of 25-watt Mazda light on the direction of movement in four leeches of the species *Glossiphonia stagnalis; b* and *b'* representing the aberrent behavior of a single individual.

The responses of the leeches to light appear fundamentally the same as those recorded by Parker and Arkin (1901), Adams (1902), Holmes (1905), and Harper (1905) in the case of the earthworm. There is combined a certain degree of direct turning with a large degree of random movement, the path of the leech away from the source of light representing the resultant of these two factors.

6. Effect of Currents

As has been previously pointed out, the specimens of *Dina* used in this work were secured from a fresh-water pond located in among the foothills of the Coast Range Mountains. Except in the rainy season, no currents are likely to be produced in the pond, which contains in its deepest part only a few feet of water. It was rather interesting to note that specimens reared under these conditions, even the young, only a couple of months old at the most, which had not passed through a rainy season, showed a distinct positive rheotaxis.

Allee (1912) has pointed out the fact that Allen found the current set up in a circular pan by stirring not to be straight, but that of a diverging spiral. Comparison of the responses of isopods in the straight and spiral current showed in his tests only negligible differences. In the case of *Dina microstoma*, I found the rheotactic responses under the stimulus of a straight current to be even more markedly positive than they were in the circular current. This result is perhaps to be explained as due to the fact that the circular current induced was very much stronger than the straight current used. The circular current, as the most convenient, was adopted in the following experiments on rheotaxis.

Five individuals which had been in the laboratory only about three days were subjected to a current induced in a glass dish 25 cm. in diameter, containing about 6 cm. depth of water. The leeches were tested one at a time for twelve trials of a minute each. The current was produced by briskly pushing a glass rod 1 cm. in diameter around near the edge of the dish for eight times. The accompanying table (Table II), the column indicated (+) denotes the number of seconds of the minute period

that the animal swam against the current; that under the heading (—) negative shows the period during which the animal swam with the current; and (±) indifferent, the length of time that the specimen hugged the bottom of the dish, going neither one way nor the other. It was necessary at the beginning of each experiment to make the current strong enough to release the hold of the specimen on the bottom of the dish.

TABLE II

Rheotactic Responses in Seconds of Five Specimens of *Dina microstoma*

No. of test	Individual I			Individual II			Individual III			Individual IV			Individual V			Average		
	+	—	±	+	—	±	+	—	±	+	—	±	+	—	±	+	—	±
1	55	5	0	45	5	10	35	5	20	40	10	10	30	10	20	41	7	12
2	45	5	10	55	0	5	35	10	15	35	5	20	55	5	0	45	5	10
3	52	3	5	50	5	5	30	15	15	35	0	25	35	20	5	40.4	8.6	11
4	58	0	2	50	0	10	40	10	10	40	10	10	10	10	40	39.6	6	14.4
5	55	5	0	20	10	30	50	5	5	20	30	10	40	5	15	37	11	12
6	48	0	12	55	0	5	40	5	15	45	15	0	40	10	10	45.6	6	8.4
7	10	5	45	50	10	0	50	10	0	25	0	35	50	0	10	37	5	18
8	30	25	5	45	0	15	55	5	0	50	10	0	20	25	15	40	13	7
9	55	5	0	50	5	5	55	5	0	45	10	5	25	20	15	46	9	5
10	57	3	0	55	5	5	50	10	0	30	25	5	30	20	10	44.4	12.6	3
11	45	5	10	35	5	20	55	5	0	40	15	5	55	5	0	46	7	7
12	50	5	5	50	5	5	45	15	0	35	10	15	50	10	0	46	9	5

Observation of the preceding table indicates the strongly positive character of the rheotaxis of *Dina*. The animal responds by swimming for the greater part of the time vigorously against the current. This positive rheotaxis is probably of considerable significance to the animal. The usual habit of *Dina* is quiet ponds, or near the edge of fresh-water lakes under stones. A positive rheotaxis would tend to keep the animals in such localities where they bred. Young individuals, one-eighth the size of the adults, showed responses as decided as the older ones.

No experiments were conducted to determine the rheotactic responses of *Glossiphonia stagnalis*, since in this form there is no swimming reaction and the principal effect of the current would be to make the animal hug the bottom of the dish.

7. Chemotactic Responses

In the experiments with chemicals, the tests were all made with a half dozen individuals for each chemical, the leech being placed in a separate glass dish. Before a different strength of the same chemical was used the leech was placed for a few minutes in clean water. The substances were allowed to diffuse into the water from a capillary pipette, the rate being so regulated as not to produce a response from the current. This can be done by gauging the size of the opening of the delicate capillary tube.

Nitric acid, acetic acid, sodium chloride, copper sulphate, and cane sugar were the substances used. All strengths of nitric acid of a greater intensity than 1/80 per cent produced a negative response. To dilutions less than this, an indifferent reaction was observed. Acetic acid revealed a similar condition at 1/30 per cent; sodium chloride at 1/5 per cent; copper sulphate at 1/320 per cent. Copper sulphate even in small quantities produced a very marked effect on the leech, producing swimming and a long continued activity. Cane sugar in an intensity of 5 per cent produced no response that could be interpreted as either negative or accentuation of positive reaction. The response to the injurious chemicals localized in this way is as decided as in the case of localized contact stimulus.

As would be conjectured, the animal shows a directly positive reaction to diffusing snail juices. The nature of this has already been described in the discussion of the feeding of leeches. Best results are secured when the food juices are fairly strong in concentration, and placed relatively close to the anterior end of the body.

The significance of these results lies in the fact that the animals respond negatively to chemicals of an injurious nature in just as adaptive a manner as to contact stimuli, turning sharply away, and if the stimulus is a strong one, swimming rapidly out of the unfavorable environment. To chemical stimuli of such a nature as those found in its food material, the *Dina* responds in a positive manner.

8. Reactions to Gravity

In collecting material for this work, it was observed that the most successful place for dredging for the *Dinas* was on the bottom of the pond. When brought into the laboratory, and placed in aquaria, the leeches crawl around on the bottom of the jar or rest quietly in masses underneath stones. It is rather rare that a specimen of *Dina microstoma* is to be seen on the sides of the aquarium; however, this is not true with *Glossiphonia*, since when the influence of light is removed these forms frequently collect in groups along the sides of the jar. When a *Glossiphonia* is placed on a vertical glass plate, however, it will usually incline downwards and crawl to the bottom of the dish. A *Dina* placed in a glass tube bent at right angles, and submerged in the water, will in the majority of cases come to rest in the horizontal portion. These observations lead one to the conclusion that this species is normally positively geotactic. Under certain conditions, there seems to be a tendency towards the reversal of this reaction. In his work on the leeches of Japan, Whitman (1886) says: "I have never seen the land leech of Japan on trees, and I believe it keeps itself habitually on the ground, or in the moss, or under damp leaves and loose rubbish. When awakened by the footsteps of man or beast it quickly appears on the surface, and frequently ascends low plants and occasionally perhaps trees in search of the intruder."

When stimulating a specimen of *Dina microstoma* to induce fatigue it was observed that there was manifested more than a dozen times the attempt on the part of the animal to crawl out of the dish. This suggested that what appeared to be a reversed geotaxis might be a tendency for the animal to crawl out of an environment unfavorable to it. So jars filled with, and inverted in, water boiled for thirty minutes and cooled in a corked flask were supplied with a number of leeches. Increase of undulatory movements was observed, but the reduction of oxygen seemed to have no effect on the geotaxis of the animal.

Not so with mechanical shocks, such as jarring. Dozens of times it was noticed in the aquaria on my laboratory table that when these were shaken by a sudden jolting of the table large

numbers of the *Dina* would begin to crawl up the sides and corners of the dish, squirming and twisting over one another. The same result was secured in jars placed on a springy board and jarred several times repeatedly. This tendency does not persist for any great length of time; for the animals release their hold in a few minutes and either drop to the bottom of the dish to crawl around or swim about as is their usual reaction when in a fairly active condition. A second heavy jar or series of jars produces nothing like so marked an effect, the animal apparently regaining its normal equilibrium rather quickly.

When a half dozen specimens were placed in water of 36° C they became exceedingly active. They would settle to the bottom of the dish often, and, executing random movements, would either move off rapidly by looping or giving the swimming response. Even water cooled to several degrees lower gave no evidence of the tendency to produce reversal of geotactic response. The effect of the heat seemed to find expression in the increased activity of the individual, and the accompanying excess of random movements.

It is rather interesting that in two forms as widely separated in habits as are the land leeches of Japan and the *Dina* of this country, a purely aquatic form, there should be the same tendencies of behavior in this regard, even though the tendency to reversal is not nearly so pronounced in the nephelid as Whitman has described it for the land form.

The blood-leeches seem to show an indifferent geotactic response when kept in aquaria. A dozen specimens kept under observation for several months in the laboratory were noted to lodge themselves out of the water almost as often as they remained immersed in it. When out of the water they suspend themselves by the two suckers, either stretching in a straight or curved position along the sides of the dish, draping themselves in a not ungraceful festoon from the under surface of the cover of the jar.

9. Influence of Heat

No attempt was made to determine the optimum temperature conditions of the leeches. In *Dina microstoma* temperatures as low as 10° C, when continued for several hours lower decidedly

the responsiveness of the animal. To a localized application, by means of a capillary glass rod, of water heated to 70° C, a negative response with an accentuation of random movements is produced. To a higher temperature, 90°–95° C, a sharp negative response accompanied by the swimming reaction is the usual habit. As already stated, the effect of a uniform temperature of 36° C is to produce a markedly increased activity of the animals subjected to it. When currents of heated water were induced in a long, shallow dish by immersing a flask of water heated to 90° C, a tendency was observed for the animals to collect in the regions of lower temperature, thus seeking as nearly as was possible their optimum temperature conditions.

10. Thigmotaxis

The strongly positive thigmotactic propensities of the leech have already been mentioned as a factor in the formation of collections. Positive thigmotaxis is still further evidenced in the large number of individuals that will find shelter underneath a small stone. When placed in an aquarium with mud and decaying vegetation in the bottom, *Dina* is often observed with two-thirds of the posterior part of the body buried among this debris, the anterior end projecting and exercising undulatory movements.

To a localized contact stimulus applied to the anterior end the usual response is a turn in the direction opposite to that of the stimulus. This varies rather widely under successive stimulation and other factors discussed in a later section of this paper. There is considerably less variability in response to stimulation of the posterior end. In the posterior end stimulation, the response is either by "looping" or by "swimming," just which response is given depending upon several factors discussed in the second portion of this paper.

11. Ability to withstand Desiccation

In most localities it would be comparatively rare that the species *Dina microstoma* or *Glossiphonia stagnalis* would have to undergo desiccation in its native habitat, and it is very fortunate for the species that this is true. Within a relatively few minutes

after having escaped from the aquarium *Dina* will dry to such a state that it is beyond recovery upon being placed in the water. There seems to be no characteristic posture assumed in the drying up of this species. The body is twisted into various shapes as the final result of the desiccation, the most common one having the anterior and posterior tips drawn in towards the center of a semicircular arch formed by the body. During the process of drying the nephelid is often exceedingly active, the contraction of the muscles of the body, affected by the drying, forcing the animal to assume widely different attitudes successively.

Frequently when removed from the water, *Glossiphonia* will roll itself up in the "pill bug" fashion, and consequently is able to withstand considerably more exposure to drying influences than *Dina*. However, the ability to withstand desiccation is not a well developed feature of the repertoire of either of these two genera.

VI. SPECIAL FEATURES OF BEHAVIOR IN LEECHES

1. Modifications of Behavior During the Breeding Season

Unfortunately, among the hundreds of *Dina microstoma* kept under constant observation in aquaria, no egg cocoons or other signs of breeding were observed. The only recorded observations on the breeding behavior of the nephelid leeches that I have been able to find are those of Iijima (1882). This worker noted what he construed as abnormal copulation, but which was later interpreted by Whitman (1891) as hypodermic impregnation through the agency of spermatophores. Quoting from Whitman: "Although it is well known that spermatophores are of general occurrence among the invertebrates, and even among many vertebrates, the assertion that, as a perfectly regular and normal affair, in animals as highly organized as the leeches, they represent an injecting apparatus by means of which the spermatic elements of one individual are forced through the body wall of another at any point whatsoever, may appear almost incredible, even when supported by direct observation many times repeated

on different species. That such is certainly the case, however, is very easily demonstrated and one can verify it as often as he likes on almost any species of *Clepsine* that happens to be accessible."

Houghton (1863) early recorded the fact that some of the *Glossiphonidae* possess the rudiments of an "incubating" and "parental" instinct. Castle (1900) records several observations in regard to the egg-laying process in the species *Glossiphonia stagnalis*. In the vicinity of Cambridge, Massachusetts, he notes the egg-laying period as being chiefly in the months of April and May, though extending to as late as September. The eggs are attached in groups to the under surface of the body. Each group is enclosed in a delicate transparent sac, these sacs being arranged in two longitudinal rows placed close together. The egg-laying occurs at night in animals kept in aquaria and was not observed. The number of eggs laid appears to depend upon the size of the animal, varying from sixteen to forty-five in number, with an average record of thirty-one.

Castle (1900) says with regard to the mode of fecundation in *Glossiphonia stagnalis:* "Whitman (1891) has shown that in the case of *G. parasitica* (*Clepsine plana*) the contents of the spermatophore pass through the integument into the body cavity, and that impregnation probably occurs while the egg is still in the ovary. A similar process doubtless occurs in the case of *Glossiphonia stagnalis*."

Moltschanov (1911) has recently given his observations on some features of the breeding behavior of certain European species of the genera *Glossiphonia* and *Hemiclepsis*. He finds upon sectioning the body of adults of these two genera that there are modified epidermal cells, which in their arrangement permit of the more ready and effective attachment of the suckers of their young. He also suggests as probable that the young derive their sustenance for the first third of their growth period from the secretions of the ventral secretory cells of the adult body. As evidence of this he records that the young can live only a short time when removed from the parent body. Bolsius (1911) mainly confirms the results of Moltschanov. He believes, however, that the mortality among the young as the result of removal

from the body is due to insufficient aeration. The parent with its young attached frequently performs undulatory movements, which provide the young animals with the necessary oxygen supply.

Castle (1900) has pointed out that in *Glossiphonia stagnalis* "the time of egg-laying, as well as of spermatophore formation, depends upon the warming of the water in the spring. One can hasten both processes by bringing the animals for a few days into a heated room." My experience in Berkeley has been much the same. In early December, on January 2, and February 18 several dozens of specimens of *Glossiphonia stagnalis* were collected from Stow Lake, Golden Gate Park, San Francisco, and placed in aquaria in the laboratory. These specimens were examined carefully when collected, and were found to carry no eggs or young. After having been in the laboratory for several days the leeches were again examined, and a few of them collected at each of these dates were observed to have eggs attached to their ventral surfaces. Specimens collected in the months from August to the middle of November were found many of them to have eggs or young attached. This would indicate that the lower temperatures cause the cessation of breeding. A somewhat extensive breeding season would seem necessary to account for the literal millions of specimens of this species inhabiting the stones along the edges of this lake, in the shallower water.

The fact that a form as low in the scale of life as the leech is to be found carrying eggs in the same manner as does *Glossiphonia* naturally arouses the question as to the possible occurrence of a "parental instinct" in its simpler expressions. Several individuals of *Glossiphonia* were secured carrying eggs attached to the ventral surface. These eggs were contained in sacs, as described by Castle (1900), some four to six usually, and totaling a varying number from twenty-one to thirty, with sometimes a few more. With a blunt-pointed needle these sacs of eggs were removed, and immediately placed, together with the individual from which they were taken, in a small glass dish 3 cm. in diameter. Careful count was made of the eggs separated in order to prevent any error which might arise through the laying of more eggs. When coming in contact directly with the eggs the

leech crawled by them or over them with entire disregard. In cases where the parent was left in the dish with the eggs for sixteen hours, and in one case for four days, not a single egg was picked up or the mass of eggs brooded over, even when placed in the least lighted portion of the dish. The stimulus of the removal of the eggs caused at first a marked activity, but later the animal was restored to the normal rate of activity, and even then the eggs were as markedly disregarded as if they had been debris in the dish. Thus the entire neglect of its eggs on the part of the parent was several times proved distinctly.

In other specimens with eggs attached, a part of the mass was loosened up so that a few of the eggs dropped out and many of them were hanging to the body. The only response was a more contracted condition of the body in the region where the eggs were carried. In this case there was also an acceleration of the activity due to the stimulus of the removal of the eggs. The local stimulation of the part of the body from which the eggs were partially removed may satisfactorily explain the local contraction of the body at this point. Although observed at intervals of a few minutes for four hours, no reactions other than this local contraction and initial acceleration of movement were observed, and these conditions became normal within a half hour after the experiment was begun. The carriage of the eggs is to be viewed as a more or less forced condition on the part of *Glossiphonia stagnalis,* due to the fact that they are enclosed in sacs attached to the body.

When the eggs are hatched the young are carried in much the same place as the eggs. These young individuals are strongly attached by the posterior sucker of their bodies. Removing the young produces, as in the case of the removal of the eggs, an active condition of the animal which seems to be entirely due to the mechanical stimulation of removal, since the specimens become normal in their responses after a period of a few minutes.

Into a small dish 3 cm. in diameter were placed an adult *Glossiphonia* and its detached young. The small leeches are very quick to seize the opportunity of attachment, and often cling to various parts of the body of the parent species. Upon their attaching themselves to the dorsal surface of the body, particu-

larly the anterior end, the parent was observed many times twisting itself almost into knots in order to get rid of the young, sometimes very successfully doing so. However, three hours later all of the young were securely attached by their posterior suckers to the ventral surface of the body of the parent. This was undoubtedly accomplished by successive attachment on the part of the young and removal of them by the efforts of the parent, until as its body passed over the young these attached themselves finally in the proper manner and could not be successfully dislodged by the parent form.

Thirteen young, the burden of a single individual, were separated from their parent and in the dish with them was placed an individual of the same species, which, however, when collected, was found to be carrying no young. The small leeches attached themselves to this adult quite as readily as to their parent, and upon becoming attached to the foster-parent remained in this position for four days, as long as the experiment was continued. This shows thoroughly that there seems to be present no attraction to the mother, but that any adult specimen, so long as it is a *Glossiphonia stagnalis*, serves to afford as effective and satisfactory a lodging place as any other of at least the same species.

In order to test this point further, thirty specimens in the aquarium were examined to see how many carried young. Out of this number, thirteen carried young, seventeen being without such a burden. The number of young carried by the different individuals varied from as few as one to as many as twenty-five. Of the thirteen carrying young, two were observed carrying one, and as many carrying three and four respectively. The others carried a larger number. These results indicate no choice of parents within the limit of the species, nor any other alternative on the part of the adult than to carry the young when they become successfully attached to the ventral surface. I have several times observed fair sized young attached to the ventral surface of adults carrying eggs some stages before hatching. Oftentimes the load of a single individual is made up of young of varying sizes, another piece of corroborative testimony.

This strong positive thigmotaxis of the young is indeed a very adaptive trait, and the persistency with which they will

repeatedly attach themselves is also a feature in their favor. In the absence of an adult form, the young collect in groups on the bottom of the aquarium just as do the older specimens. In the young of *Hemiclepsis occidentalis* this reaction is just as pronounced as in those of *Glossiphonia stagnalis,* though I have not collected the adults of this *Hemiclepsis* in groups such as *Glossiphonia* forms. It may be, however, that where they occur abundantly the formation of collections may also take place in this species. In one dish, forty-three young of *Hemiclepsis* were placed, and these formed two groups which were not dispersed during the two weeks in which the experiment was continued. Any disturbance of the dish, such as jarring or blowing on the surface of the water, caused a vigorous waving of the anterior end of their bodies, as if they were searching for the disturbing factor.

A large specimen of *Hemiclepsis occidentalis* carrying the forty-three young above mentioned was first separated from its young. In the dish with these young of *Hemiclepsis* was placed an adult *Gl. stagnalis* which formerly had been carrying young, but from which this encumbrance had been removed sufficiently long for the animal again to become normal in its movements. After remaining in the dish eighteen hours with the young, these several times being aroused to activity, this adult *Glossiphonia* did not carry a single one of the young *Hemiclepsis.* The original parent was now placed in the dish, and within five minutes two of the young had found their nestling place on the parent *Hemiclepsis.* Twenty minutes later a total of eight was found attached, the others having become massed along the sides of the dish.

The movements of the larger species, adult as well as young, are somewhat slower than those of *Glossiphonia,* and it was thought that here might be a possible explanation of the difference in the behavior of the young towards adults of two different species. Two specimens of *Glossiphonia* were decapitated, and necessarily, after a short time, little movement resulted. Although the young of the larger species were kept moving actively about the decapitated specimens, none attached itself to the body of these leeches of a different genus.

Next, the *Hemiclepsis* was placed in the dish with fifteen young of the smaller and more active forms. After four days of this combination had elapsed, none of the young of *Glossiphonia* showed any more fondness for the foreign foster-parent, as evidenced by permanent attachment, than its young had evidenced for *Glossiphonia*. While none of the young of *Hemiclepsis* were observed to attach themselves to the adult *Glossiphonia*, the reverse condition was noted in a few cases. The young of the glossiphonid in crawling about in the dish would come in contact with the body of *Hemiclepsis* and would sometimes attach themselves to the dorsal surface. The adult specimen would under such a condition soon come to rest, the lateral margins of the body closely pressed against the bottom of the dish. In this way the young glossiphonids were prevented from attaching themselves for permanent lodgment, and would soon leave the body, and finally join the collection already made by the other young in the angles of the dish.

Thus on the part of the parent forms no evidence of a parental instinct seemed present. There is recorded at least one species of *Glossiphonia* (Bolsius, 1911; Houghton, 1863) that seems to lay its eggs on some foreign object, and to remain over them after deposition until they are hatched. Gibbs (1897–1899) notes a similar behavior in the skate-leech, *Pontobdella muricata*. Whitman (1878) says of *Clepsine marginata:* "The worm remains over the eggs, for the purpose of protection only, till they hatch. The young, soon after exclusion, become fixed to the ventral side of the parent, and are thus borne until they are fully developed and able to provide for themselves."

In these cases, there does seem evidence for at least a rudimentary "brooding" or "incubating" instinct. Unfortunately, none of these forms was available for experiments in this connection. The chief eagerness for protection in *Glossiphonia stagnalis* and *Hemiclepsis occidentalis* was manifested on the part of the young in the form of strongly positive thigmotactic reactions. The discrimination on the part of the young of *Hemiclepsis* for the parent form of their own species as contrasted with that of a related one is very probably much akin to the recognition of the adult forms for their own species in the process of spermatophore deposition.

2. Diurnal Rhythmical Behavior

The leeches experimented with in this work, as has been stated, are under normal conditions negatively phototactic. This is well evidenced by the fact that they persistently remain underneath stones or among the debris of their environment during the day. Upon coming into the laboratory at night I observed many times that the leeches of both of the genera *Dina* and *Glossiphonia* were crawling actively about in the aquaria. In many instances the glossiphonids were observed by the hundreds crawling about on the sides of the dish, exercising undulatory movements, or sometimes moving along underneath the surface film much in the same manner as does the fresh-water planarian. *Dina* was usually to be found crawling about on the bottom of the dish.

The diurnal rhythm appeared so pronounced in *Glossiphonia stagnalis* that it was thought worth while to test its possible persistence under uniform and constant conditions of illumination. When a jar containing several dozens of adults was placed under constant light in a dark room it was found that the leeches remained underneath the stones in the dish for as long as a week, the length of the experiment. Observations were made daily at intervals of a few hours from eight o'clock in the morning to a varying period of nine to eleven in the evening, and it was very rarely that a single specimen was found active in the dish.

The jars of specimens kept under constant darkness showed, within a half hour after being placed in the dark room, a very noticeable activity and movement of many of the leeches to the sides of the dish. This response was found to continue for several days, not any of the leeches, however, continuing active during the whole of this period.

These results seem to indicate that the diurnal rhythm in these forms is very largely the result of the direct action of light. However, certain other factors must play an accessory rôle in the production of periods of rest and activity. Thus fatigue as the result of continued activity would cause the animal to come to rest in conditions of either darkness or light. Satiety would have much the same effect, as is shown in experiments

discussed in a later portion of this paper. On the other hand, hunger, by producing a condition of increased irritability in the organism, would tend within certain limits to cause activity resulting in what might be called a search for food.

3. Behavior of the Young Leeches

The reactions of the young of *Hemiclepsis* and *Glossiphonia* when only about two millimeters in length are, with few exceptions, essentially the same as those of the adult specimens. The normal activity of the young is marked by a somewhat greater irritability than is the case in the older forms. This fact is very clearly indicated in the excess of random movements in the process of locomotion of the young. The response given by the young to localized contact stimuli are the same as those described for the adult forms in a previous portion of this paper.

The positive thigmotaxis, so well developed in the adult leeches, is even more pronounced in the young individuals of the two genera studied. This is shown to a marked degree in the young of *Hemiclepsis*. It was unfortunate that only one specimen of this species carrying young could be secured; however, the forty-three composing its burden provided a sufficient number to permit of the observation of many features of their behavior. When removed from the body of the parent, and placed in a separate dish, the young would usually cluster in one or two groups, their posterior suckers attached side by side to the bottom of the dish. In such a position the young were allowed to remain for a couple of weeks. They were observed rather frequently during the day, and sometimes in the evenings. So far as noted, scarcely a single specimen released its hold on the substratum. The slightest jar of the table would set them to waving their anterior ends about in the dish, as if searching for the intruding factor. Soon, however, they would again settle down to a comfortable repose. This grouping, in so far as relative position of the bodies of the young to each other is concerned, is practically the same as that which is found among the young while attached to the under surface of the body of the parent.

In the young of this same species, the deceptive quiet reaction was secured upon contact stimulation just as in the case of the older specimen discussed in a preceding section of this paper. One young specimen was observed to remain perfectly quiet for as long as eight minutes after being lightly stimulated with a fine bristle attached to a wooden handle. Further light stimulation of a young leech, when placed in this condition of deceptive quiet, does not produce more than a local contraction, in most cases, just as was found to be the case with the adult specimens of this same species.

The young of *Glossiphonia* were secured in much greater abundance than those of *Hemiclepsis*, and thus permitted a more thorough study of their responses. The young of this species are hatched in egg sacs as previously described. Upon the disintegration of these sacs the small leeches attach themselves by their posterior suckers to the ventral surface of the parent leech. In this position they are carried until they reach a considerable size. I have not been able to determine just what is the cause of their "weaning," though it no doubt is to be explained as the resultant of two or three factors. One of these is the decreased thigmotactic response of the young specimen as it becomes older. Another factor is a purely mechanical one; the increase in size causes the young to become a serious impediment to the progress of the parent, and the larger size makes the burden easier to be rubbed off. Then, too, there is a limited space for the carriage of young as the result of their increase in size. This is obvious from the fact that the older the specimens of young carried, usually the smaller the number of young to be found attached.

The formation of collections in the young, scarcely more than one or two millimeters in length, when removed from the body of the parent, is as clearly pronounced as we find it in the adult glossiphonids. The formation of one of these collections is a very interesting performance to observe. Some eight or ten dozens of young of varying sizes, taken from several parents, were placed one afternoon in a small circular glass dish. By the next morning they had grouped themselves into three collections in the angles of the dish. These groups were broken up

and the formation of a new set of collections observed. The young would, in some of the cases, attach themselves to the bodies of other young, a lively squirming resulting in the endeavor of the afflicted specimen to get rid of the imposed burden. The impediment afforded by the attached leech caused a slowing of movement of the specimen carrying the load, and finally a cessation of movement of the two. With this as a starting point, a group of some thirty or forty specimens was formed. In other cases, a specimen moving about would come in contact with the dish where the bottom and sides meet, and the region being one of low light intensity, the young individual would come to rest, and from this as a starting-point a collection would be built up.

The position of one of the larger of these groups was so shifted that the young leeches composing it became subjected to the influence of strong sunlight. The result was a slow disintegration of the collection, many of the animals composing it moving, after a series of random movements, into a less lighted portion of the dish. Some of the individuals remained in the group, however, for a couple of hours in the intense sunlight, failing even to move to a region of less heat and light, the thigmotactic proclivities clearly overcoming the tendency towards negative phototaxis.

In the groups formed the young were observed to execute undulatory respiratory movements just as did the parent form. No new type of locomotor response, in so far as the free movements of the young are concerned, is to be noted in the young as contrasted with the old, though the habit of having themselves carried around is a trait peculiar to the young.

Moltschanov (1911) has found in specimens of *Glossiphonia* and *Hemiclepsis* that the young when removed from the body of the parent continue to live for only a short time. This observation he cites as evidence supporting the conjecture that the young of these two genera are nourished for a part of their existence by a secretion from the cells of the ventral surface of the parent body. Bolsius (1911) rather refutes this idea and would explain the condition as resulting from insufficient oxygen supply, since the parent form aerates the young during its own undulatory movements.

In the dish with some young of *Glossiphonia stagnalis* I placed a living earthworm, the young leeches being first aroused from the groups which they had formed. The same tendency to hang on as that which enables the young to secure its hold on the mother served in this case to cause it to attach itself to the worm. When the animals became attached to this they fed just as do the older leeches, the outline of the digestive tract standing out a vivid red from the blood contained in it. When they had become "full" they left the worm and formed collections around the edge of the dish. Within a few hours after the worm was placed in the dish, of the five or six dozens of young leeches, fully two-thirds of them showed upon examination that they had fed upon the worm.

These young after having been fed only once in this manner were kept alive with only a few changes of water in the dish for over a month. The fact that this can be done, and that the young leeches perform undulatory movements for respiration themselves, would seem sufficient evidence to dismiss as improbable the view held by Bolsius (1911) that the death of the young leeches removed from the body of the parent results from the lack of oxygen. Lack of food would seem a more important factor, since with this supplied they are able to live for over a month, or with sufficient trouble can, I believe, be reared to maturity. Whether the food of the young is partly derived from the secretions of the parent as suggested by Moltschanov is a matter which I have not been able to settle. A number of leeches carrying young were supplied with several earthworms as food, and after the parents had fed to satiety the young carried on them were examined. Several of them were found to contain blood in their digestive tract. Thus it is probable that the young gain a certain amount of their nutriment in this manner. Also they are undoubtedly able to be separated from their parents by attaching themselves to the food upon which the parent may be feeding, and upon securing a sufficiency they may find their way to a place of refuge and comfort upon some other foster-parent which may happen to pass their way. Bolsius (1911) states that he has observed young leeches to leave their parent and find their way back again to the same individual

which they left. This is not at all impossible, but is, I believe, more likely to be the result of accident rather than any selective action for a certain parent on the part of its young.

4. Operation Experiments

The anterior ends of a couple of dozens of specimens of *Dina microstoma* were removed at various distances along the body length. These operated specimens were allowed four or five days for recovery from the shock effects of the decapitation before experiments were conducted on their behavior. Observations at this time showed little difference, except for vigor, in the character of responses as contrasted with that five months later. Loeb (1894) states that he has kept operated leeches for a year without regeneration: "Schneidet man einen Blutegel in der Mitte entzwei, so zeigen die beiden Stücke durchaus verschiedene Reaktionen. Die Wunde heilt sehr bald und die Stücke können ein Jahr und länger leben, ohne dass jedoch, wie bekannt, irgend welche Regeneration stattfindet." Morgan (1901) says with regard to regeneration in leeches: "A leech is not much more complicated than a marine annelid, yet it has little or no power of regeneration." Gluschkiewitsch (1907) states in a preliminary report that he finds in the young of *Clepsine* (*Glossiphonia*) *tessulata* a regeneration of both the anterior and posterior ends. Adult specimens were not used in the experiments, and this fact may afford the basis of the difference between his results and those of other workers. He says: "Nach 23 Tagen waren unter den am Vorderende amputierten Individuen drei vollständige und fünf unvollständige Regenerate zu sehen." Hirshler (1907) found from sections of operated adult specimens that regeneration to a slight degree occurred in *Nephelis, Clepsine* (*Glossiphonia*), and *Hirudo*. The process, however, amounted to little more than a wound closure.

Although regeneration was not made the subject of any series of experiments, some observations were incidentally noted in this regard. Many of the specimens decapitated have continued

alive and in good condition for six months. No perceptible signs of regeneration appear in any of the individuals, neither the anterior nor the posterior end regenerating new segments. No sections of the leeches have been made to determine to just what extent regenerative processes have taken place. Not all of the specimens operated upon have survived for as long as six months, the mortality being approximately seventy-five per cent. The wounds of the surviving specimens have in practically every case entirely healed over. What the result of such operations might be upon subsequent regeneration in young *Dinas* is a matter of uncertainty. The work of Gluschkiewitsch (1907) is certainly suggestive in this regard.

When approximately the first eight anterior segments are removed from the body of *Dina microstoma*, the operation has the effect in most cases of setting the animal to swimming vigorously about in the dish. After a short period, the decapitated specimen settles to the bottom, becoming attached by the posterior sucker, the body stretched along the bottom of the dish. Except for a slight occasional movement of the anterior end, here it may remain for many hours.

A slight stimulation of the posterior end of such an animal produces an unequal contraction of the dorsal and ventral longitudinal muscles of the body, causing the leech to become arched, and its anterior end to be pressed against the bottom of the dish. Since the anterior sucker is not present, progressive movement cannot be made effectively by looping; so the muscles are relaxed, and the body assumes its previous position. In some cases, the pressure of the anterior end against the substratum affords sufficient leverage for the animal to drag its posterior sucker forward a short distance. This would seem to indicate that the mechanism for forward movement by looping is present except for the anterior sucker. The lack of this produces a clumsiness of response, but the reflexes constituting the movements of this type are all present in the decapitated specimens. The reaction of the decapitated specimens to an average stimulus is usually the swimming reflex. This is performed in a perfectly co-ordinated manner, though the blunt anterior margin forms not nearly so efficient a steering agent as does the attached graceful anterior end.

To contact stimuli of the anterior end there is a varying responsiveness and an equally varying type of response. Much of this variation is to be attributed to different recuperative capacities of the animals subsequent to decapitation. The majority of the reactions given to contact stimulation of the anterior end are turns away from the stimulus. However, all of the varied combinations of responses, such as turns toward, reversal followed by swimming, etc., are secured in operated specimens, much as in the case of normal individuals. The manner of execution of these reactions is rather clumsy when compared with the quick responsiveness of the normal active leech.

In decapitated specimens, a very striking reflex is secured which is not prominently expressed in the intact leech. Stimulation of the mid-dorsal region a few millimeters posterior to the wounded surface produces a vertical elevation of the anterior end. The glass rod may be moved back and forth along this region many times without evoking the swimming response of the animal. Were one to allow one's anthropomorphic tendencies sway, one might very readily imagine that the leech gains evident enjoyment from having its back scratched.

The decapitated leech is not altogether incapable of spontaneous movements, but certainly the removal of the anterior end has a very marked effect on the degree of the animal's activity. A specimen may remain for several days in a single attached position, performing no more than a few undulatory movements during this period. Much of this lack of internally initiated responsiveness is to be attributed to the lowered vitality of the decapitated animal. Some of it, I believe, is to be assigned to the loss of the anterior ganglionic centers. Specimens six months after operation show more decidedly this lack of movement.

Perhaps the most significant change in the behavior as the result of decapitation is the reduction of the tendency towards random movements. While not restricted to the anterior region of the body, the ability to perform these feeling movements seems to find its chief expression in the first few anterior segments. As has been stated in a previous portion of this paper, the function of these random movements is largely that of orienting the body before the attachment of the anterior sucker. With the

anterior sucker and the segments of the body closely contiguous to it removed, there is a reason for the lack of responsiveness in this regard.

The anterior end relieved of the posterior portion of the body will feed if given the opportunity, performs random movements rather in excess of the normal individual, and if consisting of half or more of the body length swims readily through the water. The looping response is performed, rather clumsily, since the animal is without the posterior sucker.

Frequently groups consisting of several decapitated *Dinas* are to be found in various places in the aquarium. To this extent the thigmotaxis of the leech is expressed. I have kept stones in the dish with such specimens for several weeks, but for some reason the leeches do not accumulate underneath these hiding places. Not so with the anterior ends, however, for these soon find the stones, and remain persistently underneath them until disturbed.

Undulatory movements of respiration are made by the various portions of the body, but not to any considerable degree. The posterior regions of the body, minus the anterior, are rather the more proficient in the performance of these movements than any other parts, though I have seen a small portion of the body without either anterior or posterior sucker undulating itself rather rapidly so as to secure more efficient aeration.

5. Function of the Brain

The function of the brain is, to a certain extent at least, the production of spontaneity of movement. This is indicated by the fact that there is a greater excess of movements of this character in the anterior ends removed from the body than in the decapitated specimens. This is markedly true even in leeches some months after operation. To a certain degree, the brain is a co-ordinating center, serving to make the locomotor responses more efficient as the result of the proper interaction of the parts producing the progressive movements.

Bohn (1907) has claimed for *Branchellion* the power of simple "phenomenes associatifs." Yerkes (1912) has found what

he considers as evidence of association formation in the earthworm. This would lead one to conjecture that the same capacity is present in the leeches experimented upon in connection with the present work. No experiments have been conducted to determine whether the leeches *Glossiphonia stagnalis* and *Dina microstoma* are capable of forming simple types of associations. It is not at all improbable that such is the case, but I see no difficulty in accounting for any of the features of their behavior on the basis of the simpler characteristics common to the behavior of the lower organisms.

B. MODIFIABILITY IN THE BEHAVIOR OF THE LEECH *DINA MICROSTOMA* MOORE

I. INTRODUCTION

As a rule, the factors which determine the behavior of an animal at a given moment are many and complex. It has been shown conclusively by numerous workers that these factors are internal as well as external. Consequently, behavior is the resultant of the action of these two classes of stimuli: sometimes the internal stimuli preponderate; again, it is the external stimuli which exercise the greatest determining influence. The complex interrelations of these two classes of stimuli make the problem of analysis of behavior a difficult, though not impossible, one. The various factors can be intensified or diminished and the effects of these changed relations observed. Observations secured under these controlled conditions will provide data which are of such a nature as to contribute much to the solution of the problem of modifiability.

With such a number of factors involved, it is evident that a wide range of variation in both degree and type of response will be the result. However, there is a limit to this modifiability, which usually is in direct proportion to the needs placed upon the organism by the varying conditions of its environment. To discover the physiological bases for these reactions, and the limits of power of adjustment of these "physiological bases," constitutes the problem of modifiability.

As to the importance of this phase of animal behavior, Jennings (1905) says: "A thorough study of the modifiability of reactions to external stimuli in lower organisms seems at present one of the great desiderata in the study of animal behavior. Recent work has been devoted largely to the study of sharply defined forms of reaction and to the discovery of conditions under which these forms appear in a typical way. As a result, there is a widespread impression that the behavior of lower organisms is

composed of invariable reflexes, occurring always in the same way under the same external circumstances. This is far from the truth and leads, as it seems to the writer, to a fundamentally false conception of the nature of animal behavior. Inner states and changes are fully as important in determining behavior as are external stimuli, modifying fundamentally the reactions which the latter produce."

The works of Jennings (1902, 1905, 1906), Bohn (1907, 1909), Yerkes (1906), Holmes (1905, 1907, 1911), Hargitt (1906), and Allee (1912) are the chief contributions to this phase of animal behavior. Considering its importance, the field is a rather neglected one, and certainly its complexity will afford work enough for some time to come. The following study was undertaken to learn, so far as possible, the general features of modifiability in the leech, *Dina microstoma* Moore. Except where specifically mentioned, no other species of leech was employed in the experiments discussed in the section of this paper dealing with the subject of modifiability.

II. DIFFERENT RESPONSES TO THE SAME STIMULUS

Every animal with any degree of complexity of structure shows a considerable variation, qualitative as well as quantitaive, to successive applications of the same stimulus. Not only is this true in the behavior of the more complex organisms, but it holds with equal force in certain of the lower forms. A case in point, which has become classic in the literature on animal behavior, is the modified responsiveness of *Stentor* (Jennings, 1906) to particles of carmine repeatedly applied to its disk. The work of Pearl (1903) has served to emphasize this feature of behavior in the planarian. Jennings (1906) has furnished a very suggestive analysis of the factors determining the direction and character of the movements in the earthworm. The leech, however, is an aquatic annelid, and its repertoire of responses differs considerably from that of the earthworm. For this reason a classification and analysis of its different reactions to the same stimulus seem desirable.

1. Reactions to Stimulation of the Anterior End

The extreme sensitiveness of the body of the leech has been considered in the first part of this paper. The animal is very responsive even to slight stimulation of any part of its body with a flexible hair bristle or a delicate capillary glass rod. In the majority of cases the response is a turn or movement away from the stimulus; yet there is a decided variation in this regard. Several different responses varying in character and degree can be secured upon stimulation of a localized region of the anterior fifteenth of the body. Some responses to stimulation of one side

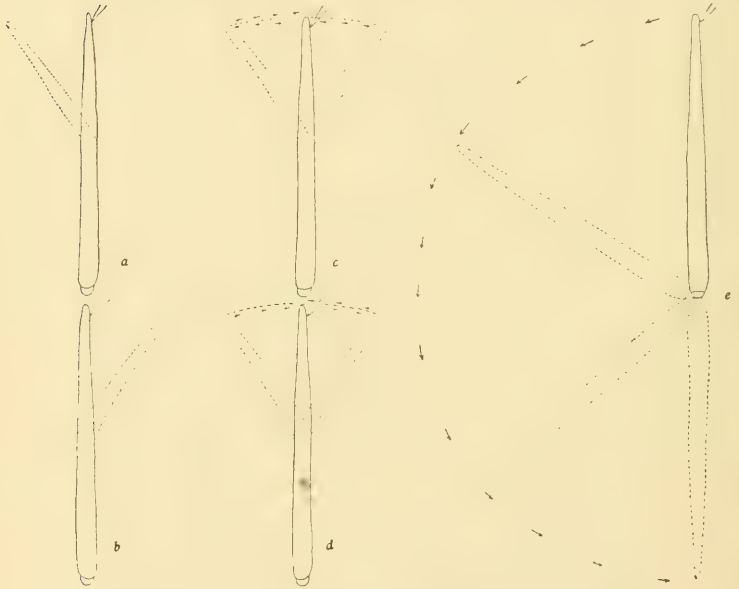


Fig. 5.—Five different responses to the same localized contact-stimulation of the anterior end of *Dina microstoma:* (*a*) turn to the left, (*b*) turn to right towards the stimulus, (*c*) turn to left followed by turn to right, (*d*) turn to right followed by turn to left, and (*e*) a complete reversal of direction by turn to left.

are listed below. These responses were secured by stimulating as nearly as possible the same region of the right side of the anterior end of the body, though this is confessedly difficult to do in as active a form as *Dina microstoma*. The stimulus was that from a flexible bristle fixed rigidly into a split wooden handle, the bristle being bent about the same degree at each application of the stimulus. In this way there was secured, as nearly as is practicable, fairly exact localization and an even intensity of stimulation.

The responses to stimulation in this way are as follows:

1. A turn to the left and movement forward in that direction.
2. A turn to the left, then to the right and forward movement.
3. A turn to the right in the direction of the stimulus and forward movement.
4. A turn to the right, followed by a turn to the left and forward movement.
5. A release of hold on the substratum and forward movement by the swimming reaction.
6. Disregard of the stimulus except for local contraction, and continued forward movement.
7. Local contraction of the part stimulated, the animal hugging the bottom of the dish.
8. A lifting of the anterior end and execution of random feeling movements.
9. With posterior end attached, a complete reversal of direction by a sharp turn to the left, followed by swimming reaction.

Many other combinations of these reactions might be mentioned; for example, reactions number one, two, and three might be performed as turns merely, not being accompanied by forward movement. It will be observed, however, that though there is a wide variation in degree and combination, the whole series can be classified as follows: (1) turns to right or left or up and down; (2) forward movements by looping or swimming; and (3) local contraction of the part affected. While it is a difficult matter to explain the order of response in each case, the knowledge of the mechanism of these reactions, as discussed in the first part of this paper, serves to suggest many valuable points toward this end.

2. Order of Response in Twenty-five Stimulations of the Anterior End

It can be seen very readily that not all of these reactions are adaptive in character, especially in the case of those which would tend to lead the animal in the direction of the stimulus. It was noticed in the various stimulation series performed in this work that the first responses of the animals which had not been stimulated for some time previously were usually such as to carry it out of the region of the stimulus. This condition was, however, far from invariable. With the idea of determining the relative frequency of the non-adaptive responses, the reactions of six individuals to twenty-five successive stimulations of the character above indicated were recorded, and the more common types of response tabulated.

The entire record of Individual one is given, since to do this is to afford a clearer idea than would any attempt at a description of the general character and order of response. The stimulus in each case was applied with a delicate glass rod and to the right side of the anterior end of the body of the leech.

Responses of Individual I to Twenty-five Successive Contact Stimulations

1. Complete recoil by sharp turn to left, movement forward.
2. Turn to the left and back slightly to the right, movement forward.
3. Turn to left and then to right.
4. Turn to right.
5. Turn to right.
6. Local contraction of part stimulated, movement forward.
7. Turn to left and back to right.
8. Turn to left and back to right.
9. Turn to left.
10. Turn to right.
11. Turn to left.
12. Turn to left and then to right.
13. Local contraction and movement forward.
14. Turn to left.
15. Turn to left and then to right.
16. Turn to right.
17. Turn to right and then to left.
18. Turn to left.

19. Turn to left.
20. Local contraction followed by swimming movements.
21. Local contraction, moved forward.
22. Turn to left.
23. Turn to left and back again to right.
24. Turn to left.
25. Turn to right.

The accompanying table (see table III) does not attempt to show the number and succession of the entire nine responses catalogued as the result of a number of contact stimuli, but only

TABLE III

NUMBER AND SEQUENCE OF RIGHT AND LEFT TURNS IN TWENTY-FIVE STIMULATIONS OF THE RIGHT SIDE OF THE ANTERIOR END

	Number of individual					
	I	II	III*	IV*	V	VI*
Number of times turned to right in succession at different times	2	....	2	2	....	2
	2	. .	5	2	....	2
Number of times turned to left in succession at different times	2	2	4	3	2	5
	2	2	2	3	7	2
	2	2	3	2	2	6
	2	3	5	2	.. .	....
	.	2	....	2	....	....
	.	. .	....	2	....	...
	.	....	....	2	.. .	.. .
Number of times turned to left followed by turn to left	2	1	1	1	1	1
	2	1	1	2	1	5
	1	.	3	2	1	1
	1	....	....	1	1	1
	1	. ..	....	1	....	...
	...	....	....	1	....	....
	.	.. .	....	1	.. .	.. .
Number of times turned to right followed by turn to left	1	....	1	1	....	1
	....	....	.	....	....	1
	. .	....	....	....	....	1
	..	....	....	....	....	1
Number of times of complete recoil to left	1	1	. .	1	1	1
	....	1	. .	..	1	....

* The apparent discrepancy in that the number of responses sometimes totals more than the actual number of stimulations is due to the fact that a turn to the right may follow, say two previous turns to the right and itself be followed by a turn to the left. Thus the response would be classified twice. Several such combinations are possible, and it is for this reason that the total number of responses is more than twenty-five in the cases indicated by the asterisk.

the more common and important of these are given. The great predominance of the adaptive reaction, a turn to the left away from the stimulus, is very plainly indicated. A decided tendency for a reaction to be repeated several times in succession is also to be observed. The significance of these facts in the explanation of the nature of the reactions is considered in a succeeding paragraph.

3. Reactions to Stimulation of the Posterior End

To contact stimulation of the posterior end the responses are much more stereotyped, due partly perhaps to the fact that the posterior sucker is attached when the stimulus is applied. So far as I have been able to determine, there are only two types of reactions when the stimulus is applied to the posterior region of the body. These are as follows:

1. By the looping response, much as a measuring worm moves forward.

2. By the release of attachment to the substratum, and the execution of eel-like swimming movements.

The first response is that usually given upon the application of a slight stimulus to the animal when it is in a resting condition, or in a state of low sensitivity produced from some such cause as fatigue. The swimming response is the more commonly evoked, and is the expression of an active condition of the organism. The rapidity of its execution serves to remove the animal speedily from the region of stimulation.

4. Determining Factors of the Different Response to the Same Stimulus

(*a*) *Intensity of stimulus.*—It is obviously impossible to stimulate the leech each successive time to the same degree. This fact alone plays its part in determining the character of the response to contact stimulation of a certain degree, though its influence has been eliminated so far as practicable. Under uniform conditions, when the body of the animal is extended, stimulation with a fine hair bristle or a capillary glass rod on the right side of the anterior end of the body will usually produce

a turn of the body to the left and away from the stimulus. A much stronger stimulation with the animal in the same position will produce a still farther turn to the left; while a stimulus of still greater intensity may cause the animal completely to reverse its direction of movement, and combine with the turn the swimming response. A very slight stimulus applied to the anterior end while the animal is moving forward will often produce no effect further than a local contraction of the part stimulated. It has already been mentioned that to slight stimulation of the posterior end, the looping response is usually given; a much stronger stimulus will immediately evoke the swimming response.

(*b*) *Localization of stimulus.*—A slight stimulus along the extreme anterior edge of the body often produces a distinct positive response in which the animal inclines toward the stimulating rod, and applies to it the anterior sucker, withdrawing it quickly. The same stimulus applied a few millimeters posterior to this region will usually cause a turn of the body in the opposite direction. Other conditions continuing uniform, the same stimulus applied to the right and left sides of the anterior end of the leech will produce turns in opposite directions—in each case a turn away from the stimulus. Stimulation of parts anterior to the middle region of the body will usually produce a typical anterior end response, while a strong stimulus applied to the parts posterior to this will evoke the swimming response. The reactions produced upon stimulating the posterior end are, as previously stated, of a considerably less plastic nature, and of a type quite different from those usually produced by stimulating the anterior end.

These diverse types of response resulting from localization of the contact stimulus are what one would expect from an animal which is at all complex in its structure. The stimulation of a certain region affects reflex arcs so correlated in their action upon end organs that unless the normal equilibrium of the mechanism is upset usually an adaptive reaction is secured.

(*c*) *Position of the body.*—The position of the body of the leech at the time of stimulation is often a cause of differences of response. If the anterior end of the leech is inclined rather sharply towards the left, stimulation of either the right or left

side will usually produce a sharp turn to the right. If the animal is crawling forward, the anterior sucker attached, stimulation of the anterior end will produce usually only a local contraction of the part stimulated, the leech continuing its forward movement at an accelerated rate. Such modification of behavior as this holds much in common with the case of striking a man when he is stretched on the ground. He must first get up before it is possible for him to strike back effectively. The leech in crawling forward is executing, as Von Uexküll (1905) has shown in the blood-leech, a sequence of reflexes. A certain equilibrium of the body is well established through this action, which first necessitates the completion of the reaction started. This is what is usually done except when an intensely strong stimulus is applied. In such a case, the leech will release the anterior sucker immediately and swing violently away from the stimulating agent. The average strength of stimulus applied to the anterior end when the leech is crawling forward is often transformed into an accelerating factor, causing the looping response to be more quickly executed.

(*d*) *Tonus of the Organism.*—From his work on *Planaria*, Pearl (1903) concludes that the "physiological states" in this form play a large part in determining its behavior. These states he classifies as follows: a resting or sleeping condition; a normal undisturbed activity; a condition of heightened activity; and an excited condition. He also records states of hunger and satiety. Jennings (1906) gives as examples of similar states in the earthworm: the state of rest; a state of excitement; a state of greater excitement; a state of still greater excitement; and a state of still more intense excitement. This classification does not include "all physiological states resulting from varied states of metabolism, and possible lasting modifications of physiological states (habits, etc.)." The same writer says: "The movement at a given time demonstrably depends not alone on present external conditions, but also on former external conditions, former actions of the organisms, and present internal physiological conditions that are determined in many ways."

These same states are to be observed in the leech, each having its own more or less characteristic mode of response. When

the animal is in a condition of quiet or "sleep" two or three stimulations with a glass rod are usually necessary to produce a reaction other than a mere local contraction. A stage of increased tonus ensues in which the leech responds readily with vigorous turns away from the stimulus, and rapid looping movements. A still greater state of excitement follows upon continued stimulation, and in this condition the swimming response seems the dominant reaction. As is discussed in a succeeding portion of this paper, fatigue produces its characteristic depressed responsiveness. As for states of hunger and satiety, the first of these seems to cause in general a condition of greater reflex excitability; the latter, a lowered responsiveness to stimulation.

All of these described physiological states in the planarians, in the earthworm, and in the leech, seem to find their expression through a modified reflex irritability of the particular organism. They represent various degrees of excitement from that of complete depression, as in the case of fatigue, to that of the most intense excitement. If this be true, and this is the opinion of the writer, we have a very suggestive viewpoint afforded in the work of Von Uexküll (1905).

(*e*) *Chain reflexes.*—Von Uexküll has shown that in "das Gehen" of the blood-leech there is a certain sequence of reflexes involved. He says: "Es ist schon dem Augenschein nach unzweifelhaft, dass hier eine Verkettung von Reflexen vorliegt, die sich zu einem Ringen aneinanderschliessen."

Such a condition seems to explain largely the different responses to the same stimulus of the anterior end in *Dina microstoma*. The reflex ring necessary to produce such modifications would have to be little, if any, more complex than that which is used by Von Uexküll in explaining the looping response. The effectors *c* and *d* in the accompanying diagram (see fig. 6) represent a turn to the right and left respectively. Strong stimulation of an intermediate region *e* produces first a turn to the right. An overflow of stimulus set up by the turn to the right spreads back to the left and a turn to the left is produced. Thus we have the response of a turn to the right followed by a turn to the left. Such a conception would also explain why a turn to the right tends to be followed by a turn in the same direction

for several successive times. The path along the reflex ring to the particular effectors involved is made more permeable. Sherrington (1911) says: "The overflow of reflex action into channels belonging primarily to other reflex-arcs than that under stimulation leads to the production by the single stimulus of a wide, compound reflex which is tantamount in effect to a simultaneous combination of several allied reflexes."

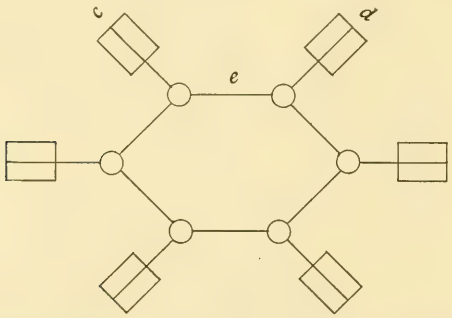


Fig. 6.—Diagrammatic representation of a nerve ring. Adapted from von Uexküll (1905).

With a nerve ring consisting of the connections for the few distinct elements of these apparently very complex movements, I believe a satisfactory explanation of the *modus operandi* is afforded. These elements would be such as a turn to the right, a turn to the left, a connecting link with a ring producing the looping response, and a similar one with the swimming reflexes. Such a view is in accord with the current nerve physiology, and makes relatively simple what at first sight appears markedly complex.

States of excitement indicate changes in the nerve centers as well as in the muscular tissues, and these changes, though ever so slight, may produce widely different responses to the same stimulus. Thus we have accounted for, on a satisfactory basis, the different reactions to the same stimulus in the various physiological states or states of excitement in the lech.

In applying the conception of chain reflexes to the responses of the leech just considered, it is well to bear in mind the qualification of Jennings (1906): "If this term [chain reflex] is used, it needs to be kept in mind that in most cases the succeeding phase is not invariably and irrevocably called up by the preceding one, as is implied by this term. On the contrary, the relation between the two is extremely variable. One type of action may be repeated many times before the second type comes into play, and the order of the different actions is by no means always the same."

III. ACCLIMATIZATION TO STIMULI

1. Acclimatization to Repeated Jars

The extreme sensitiveness of the leech to the various classes of stimuli is a very characteristic feature of the behavior of these animals, and one that is easily overlooked if proper care is not exercised. The nature of the response to a slight jar of the dish in which the animal is kept varies much with the strength of the shock, and the position and internal states of the organism. If the animal is in a resting condition, the slight stimulus of the jar may cause it to move forward by looping. If the leech is already moderately active, the stimulus may excite it to greater activity, such as swimming or more rapid looping movements. When it is executing undulatory respiratory movements it may contract and hug the bottom of the dish, later resuming the same type of reaction. Again, it may react by contraction, cease the undulatory movements, and follow up the line of orientation resulting from random movements evoked by the stimulus. The tendency towards the temporary reversal of geotaxis has been previously discussed in a consideration of the general reactions of leeches.

It is often a difficult matter to secure a leech which will continue its rhythmical movement after the cessation caused by the stimulus of a slight jar or shadow. The most satisfactory way found was as follows: Place a stone in the aquarium on the side of the dish away from the window. The leeches will accumulate underneath this shelter and, protruding the anterior two-

thirds of the body, often a dozen or more of them at the same time will be found exercising the respiratory movements. In the following experiments, an aquarium eight by nine by eight inches, containing about five inches of water, was allowed to remain for a couple of hours undisturbed on a one-inch, well-seasoned pine board sixteen inches in width and approximately seven feet in length. This board was rested on two laboratory tables six feet apart, and the flexibility provided the proper conditions for the application of a stimulus of the desired intensity.

The undulatory respiratory movements were in progress among the leeches. These movements are much like the swimming movements, except not so vigorous, the posterior sucker remaining atatched. During the execution of them the body of the leech may sway about in various directions, and often this fact proves a cause of interference in the progress of the experiment, owing to the contact of the body with that of another individual. The jar was made by tapping the board very slightly with the closed fist, allowing this to drop gently through a distance of about one foot above. By this means an approximately uniform stimulus could be secured.

It is somewhat unusual to secure a specimen continuing its rhythmical movements for several hours continuously, but this was observed in some cases. The influence of slight jars on these movements in a single leech is indicated in an accompanying table (see table IV). A slight jar of the dish was made at intervals of thirty seconds for twenty successive times, the duration of the cessation of response being measured by means of a stop watch. Several series of these stimuli were made with varying intervals between the series. Even so slight an interval as two minutes, as is shown in the last column of the table, serves to allow the animal partially to recuperate its original responsiveness.

In order to determine the range of individual variation in this acclimatization response, several other individuals were tested out at intervals of thirty seconds. Considerable variation occurs among them in regard to duration of the first cessation period and succeeding ones, some individuals acclimatizing much more readily than others. After several negative responses, the stim-

ulus may gradually be increased until the leeches in many cases will fail to respond to a considerable shock of the springboard. However, there is a limit to the degree of stimulation to which

TABLE IV

Acclimatization to Jars as Expressed in Number of Seconds Cessation of Undulatory Movements in a Single Specimen of *Dina microstoma*

Order of stimulation	(*a*) Stimuli at 30″ intervals	(*b*) 30′ after series (*a*) Stimuli at 30″ intervals	(*c*) 60′ after series (*b*) Stimuli at 30″ intervals	(*d*) 15′ after series (*c*) Stimuli at 30″ intervals	(*e*) 5′ after series (*d*) Stimuli at 30″ intervals	(*f*) 20′ after series (*e*) Stimuli at 2″ intervals
1	5	3	18	8	5	3
2	6	2	8	4	3	2
3	5	4	4	3	1	2
4	4	0	5	3	0	1
5	14	1	1	1	0	3
6	4	0	0	0	0	3
7	3	0	0	0	0	4
8	11	0	1	0	*3	2
9	4	0	0	0	0	5
10	0	0	0	0	0	0
11	0	0	0	*1	0	4
12	0	0	0	*1	0	5
13	0	0	0	*1	0	3
14	0	0	0	0	0	4
15	0	0	0	0	0	5
16	0	0	0	0	0	3
17	0	0	0	0	0	2
18	0	0	0	0	0	1
19	0	0	0	0	0	0
20	0	0	0	0	0	3

* These responses are due to the swaying of the body of another leech alongside the one whose cessation periods are recorded.

they will continue to respond by acclimatization in their rhythmical response, and as the result of a transgression of these limits reactions of the type above described, such as looping, swimming, feeling movements, or reversal of geotaxis may take place. The accompanying table (see table V) serves to show the range of individual variation in the responses of five leeches.

2. Acclimatization to Successive Shadows

If the leeches, while their posterior suckers are attached to the under surface of a stone, are exercising undulatory movements, and a black cardboard of fair size is brought between

them and the window which affords their greatest source of light, an immediate contraction is the usual response, the animal hugging the bottom of the dish. Allow the board to remain interposed until the leech has again resumed its movements and then remove the obstruction. No response to this increased intensity of light is evoked, the undulatory movements continuing. This is the same condition found by Loeb (1893) and Hargitt (1906) to hold in certain of the tubicolous annelids, where only a decrease in intensity seems to act as a stimulus to the animal. However, in the case of *Dina* any considerable increase in the intensity of light is sufficient to cause cessation of the undulatory movements, and eventually movement to a less lighted portion of the dish. A group of leeches performing these undulatory movements was illuminated with two 25-watt Mazda lights. The movements were at first rather vigorously accelerated, but later the animals completely withdrew underneath the stone or moved to a less lighted portion of the dish.

TABLE V

Acclimatization to Jars as Expressed in Number of Seconds Cessation of Undulatory Movements in Five Specimens of *Dina microstoma*

Order of Stimulation	1	2	3	4	5
1	5	30	45	10	25
2	6	8	15	8	8
3	5	12	7	5	7
4	4	7	6	32	8
5	14	4	2	5	5
6	4	0	4	2	7
7	3	6	0	2	3
8	11	0	1	23	3
9	4	4	0	6	2
10	0	12	0	3	3
11	0	0	0	1	2
12	0	0	0	1	0
13	0	7	0	0	0
14	0	0	0	0	0
15	0	0	0	0	0
16	0	0	0	0	0
17	0	0	0	0	0
18	0	0	0	0	0
19	0	0	0	0	0
20	0	0	0	0	0

In the accompanying table (see table VI), even where the zeros are recorded in the two-minute interval responses, there is to be observed in the animal a slowing-up of movement without actual cessation. Mention of the fact is made to show that even in these cases we have a partial recuperation of the original condition of the animal evidenced at the beginning of the series of applications of the stimulus. The acclimatization to shadows is to be observed as much more readily effected than in the case of slight jars.

3. General Discussion of Acclimatization Results

The phenomenon of acclimatization is such a familiar one, and the numerous cases of it have been cited so frequently in the literature on animal behavior, that only a reference to many of them is necessary to recall the details to the mind of the reader. In *Stentor* Jennings (1902) found that the first few light contact stimuli caused a contraction of the animal, but subsequent ones of the same general intensity failed to produce this effect. Wagner (1904) has shown a similar condition to hold in *Hydra*. Holmes (1911) found "that light mechanical stimulation of the anterior end of *Loxophyllum* causes at first a ready response; several repetitions in close succession diminish the responsiveness so that a much stronger stimulus often fails to produce any noticeable effect. In a few seconds, however, recovery is apparently complete, and the animal is as responsive as before." Somewhat similar phenomena have been found in planarians (Pearl, 1903), and the experiments of Mrs. Yerkes (1906) and Hargitt (1907) on tubicolous annelids have been mentioned in a preceding paragraph.

Dr. Holmes (1911) in discussing the causative factors in this type of modifiability summarizes the three possible explanations as follows: "Gradual cessation of response to a given stimulus may be due (1) to a fatigue of the motor apparatus, (2) to a dulling of the sensibility of the receptors, or (3) perhaps to other states of the organism. A considerable part of the cases of cessation of reaction to a given stimulus are possibly due, as Bohn contends, to a 'fatigue sensorielle' or dulling of sensibility.

TABLE VI

Acclimatization to Shadows as Expressed in Number of Seconds Cessation of Undulatory Movements in Five Specimens of *Dina microstoma*

Order of stimulation	Individual I		Individual II		Individual III	Individual IV	Individual V
	Stimuli at 15″ intervals	Stimuli at 2′ intervals	Stimuli at 15″ intervals	Stimuli at 2′ intervals	Stimuli at 15″ intervals	Stimuli at 15″ intervals	Stimuli at 15″ intervals
1	15	8	14	6	8	5	16
2	0	4	11	8	7	3	0
3	3	7	0	2	0	0	0
4	0	4	0	9	2	0	0
5	0	0	0	3	0	0	0
6	0	4	0	0	0	0	0
7	0	0	6	2	0	0	0
8	0	1	0	0	0	0	0
9	0	2	0	5	0	0	0
10	0	2	0	0	0	0	0
11	0	1	0	0	0	0	0
12	0	4	0	4	0	0	0
13	0	3	0	2	0	0	0
14	0	4	0	0	0	0	0
15	0	0	0	3	0	0	0
16	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0
18	0	3	0	2	0	0	0
19	0	4	0	0	0	0	0
20	0	3	0	0	0	0	0

This supposition is supported by the fact that the central apparatus is much more susceptible to the effects of fatigue than the afferent or efferent nerves. It is not a fatal objection to the theory of fatigue that the response falls off very quickly. An extreme sensitiveness may result from a certain condition of balance which a slight chemical change might overthrow without rendering the organism insensitive to stronger stimuli.''

That in the acclimatization experiments conducted on *Dina microstoma* the changed responsiveness of the organism is not due to a fatigue of the muscular motor apparatus is well borne out by the fact that after the animal has failed to respond to several previous light stimuli a stronger jar will produce a cessation of the undulatory movements. The phenomenon is very different from that involved in the death feint, where the entire state of the organism appears to be changed, as is the case in

the plum curculio (Gee and Lathrop, 1912), by a very slight contact stimulus. The changed responsiveness of the leeches to the light stimuli of jars and shadows seems to be due, then, to the "fatigue sensorielle" of Bohn, involving perhaps both a dulling of the sensibility of the receptors and slight changes in the nerve centers involved.

IV. Normal Fatigue from Repeated Contact Stimuli

The study of muscular fatigue and mental fatigue has received much consideration in comparatively recent years. The work of Mosso (1905) is a classic in this field. Lee (1907) discusses the physiological effect of paralactic acid, mono-potassium phosphate, and carbon dioxide, the substances at present known to be formed in the muscular tissues of the higher animals during fatigue. Yoakum (1909) in an extensive monograph has considered the matter of mental fatigue and gives a rather full review of the literature bearing on this subject. With regard to the phenomenon of fatigue of skeletal muscle, Ranke (1865) says: "Every one knows that the first twitch of the muscle is not its greatest. With the stimuli uniform in strength the later contractions are stronger than the earlier ones." Marey (1866) discusses the fact that in continued activity the height of the muscle curve at first increases and then decreases. Lee (1907) in a paper discussing the cause of the "Treppe" says in regard to this phenomenon: "In its literal sense this term signifies the fact that the repeated responses of a tissue to repeated and equal stimuli increase for a time in intensity. In a more general sense, the phenomenon may be characterized as augmentation of activity resulting from previous activity." He finds that the fatigue products, if present in small quantities or in moderate quantities for a brief time, cause an augmentation of activity, characterized by an increase in irritability and working power. If present in moderate quantities, or smaller quantities for a longer time, each of the fatigue substances is depressing or fatiguing.

Bohn (1909) has pointed out in *Cerianthus* among other forms that there is an increased sensibility of the tentacles to a certain stage, reactions of a certain type becoming more and more easy. When that stage has been reached there is a corre-

sponding "desensibilisation" which is pronounced in the late afternoon or evening. The results of the repeated excitation are shown differently throughout the hours of the day. To quote him exactly: "Quand une excitation se répète un certain nombre de fois, on observe souvent que pendant un certain temps la réaction devienent de plus und plus facile, c'est-à-dire se fait avec un rapidité et une intensité de plus und plus grandes. Enfin, vers le soir, au bout de quelques attouchements, le tentacle devenait insensible." This condition he suggests is to be explained in terms of the chemical equilibrium within the cells involved. It is suggested that under the influence of catalyzing agents the vigor of a certain reaction is increased, due to the liberation of the specific energies leading to that type of response. The decline in response is to be attributed to the impoverishment in the cells of these certain substances. After a period of repose the organism replenishes its supply of the substances needed and the normal response is again given.

It had been observed in some unpublished experiments of mine on planarians and earthworms that there seemed to be in their response to several hundreds of repeated contact stimuli a process very analogous to that found by Bohn in *Cerianthus*. A difficulty presented itself in these forms due to the fact that there was not even an approximately accurate method of quantitatively measuring this increase and decline of response. In *Dina microstoma,* however, the duration of the swimming response seemed to be at least a fairly accurate gauge of the degree of activity in the successive periods. Accordingly, three individuals were subjected one at a time to repeated contact stimulation of the posterior end, and the duration of the responses measured by means of a stop watch.

The results of the three were found to be very much the same. There was a phenomenon resembling in its general features the fatigue of skeletal muscle as reported by the workers cited above. There was at first a period of comparatively low response from which the animal was aroused to an increased degree of activity indicated both by the vigor of its response and the duration of the swimming period. A more accurate register of the degree of excitement of the leech would be its

vigor of response, but this is obviously a character not easily capable of quantitative determination. Following this stage of activity, in which the stimulus immediately made the animal vigorously active, and in which responsiveness continued for much longer swimming periods, was one of a somewhat slow decrease, resembling the increase in its successive gradations. This decrease is more marked from the point of view of vigor than of duration of response, since, as will be observed from the accompanying record (see table VII), progressive movement had practically ceased long before the stage at which wigwag movements had become so diminished in character as not to push the animal at least a slight distance forward in the water. When the animal reached such a stage of depression as the results of the movements evoked by the application of the stimulus, the experiment was discontinued. In the individual whose curve of

TABLE VII

Duration in Seconds of Swimming Response in Fatigue Produced in *Dina microstoma* by Repeated Contact Stimulation

Order of stimulation	Number of applications of stimulus	Duration of response evoked	Order of stimulation	Number of applications of stimulus	Duration of response evoked
1	1	5.7	23	1	19.8
2	1	5.7	24	1	19
3	1	3.7	25	1.5	14.3
4	1	10.3	26	1	20
5	1	10.3	27	1.3	22.1
6	1	11.1	28	1.1	19.3
7	1	14.5	29	1	15.3
8	1	15.3	30	1	19
9	1	11.1	31	1	29
10	1	17.5	32*	1.8	26.1
11	1	21.3	33	1.6	13.5
12	1	11.5	34	2	24.5
13	1	15.1	35	1.8	14.6
14	1	18.3	36	2	12.6
15	1	18	37	2.5	8
16	1	24	38	1.8	18
17	1	14.3	39	2.1	10
18	1	33.5	40	2	12
19	1	21.8	41	2	12
20	1	16.2	42	2.3	8
21	1	13.1	43	2	4
22	1	28	44	.....	0

* After this period little progressive movement resulted from application of stimulus.

activity is plotted in an accompanying graph (see fig. 7), some two hundred and sixty-four stimulation periods were necessary to produce the looping response. In the stage of excitement the lation required almost five hours of undivided attention on the part of the experimenter. The animal was not allowed to recuperate between stimulations, but as soon as it settled to the bottom of the dish and attached itself it was again excited to activity.

The results given in table VII are the averages derived from six successive stimulations of the series of 264. Thus number one indicates the average duration of swimming period evoked by stimuli one to six; number two, the average of stimulations six to twelve, etc. This condensation was necessary in order that the curve might be plotted on a convenient scale. Especially in the first individual tested, and to a certain extent in the other two, light stimulation of the posterior end of the animal tended to produce the looping response. In the stage of excitement the swimming response is readily given to stimulation of the posterior end, but towards the end of the series there is an outcropping of the tendency to move forward by the looping response. This made it necessary in some cases to apply as many as three or four stimulations in order to have the animal move forward by swimming. The number of stimulations necessary at a given period of the experiment is indicated in one of the columns of the table.

The condition of very indifferent progress is one in which the animal makes slow, jerky, and somewhat incoördinated movements very similar to those occurring under the influence of continued action of the various depressants tested on these forms and discussed in a succeeding portion of this paper. The muscles were, however, in a much more rigid state than in the case of strychnine and chloretone depression; but also much less tense than was the condition produced by nicotine. When allowed to remain undisturbed for a few seconds, the animal would contract, and except for an occasional side to side movement would remain in almost absolute quiet. The accompanying graph (see fig. 7), plotted from the data given in Table VII, indicates the degree of activity at the successive periods. The leeches experi-

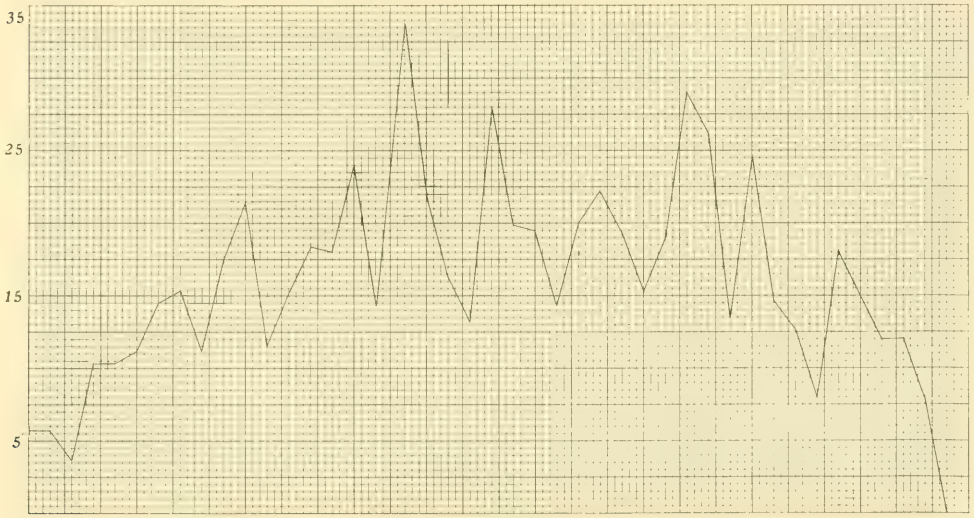


Fig. 7.—Curve of activity in leech produced by repeated contact stimulation. Scale: three spaces on abscissa represent a stimulation period; two spaces on ordinate, a second's duration of swimming response.

mented upon were allowed in each case to remain in the dish until the next morning, and in each case had practically entirely recovered their normal responsiveness.

V. INDUCED DEPRESSION

According to Cushny (1910), fatigue due to the prolonged exercise of the normal organ, and as the result of depressants, has in several instances been shown to be much the same. Quoting him: "Depression, whether induced directly or following on stimulation, has been shown in several instances to resemble the fatigue induced by the prolonged exercise of the normal organ, and it is probable that depresison and fatigue are in all instances identical in appearance, although not necessarily identical in cause."

In order to throw some light on the nature of fatigue in the leech, since this condition seems an important factor in the explanation of some of the features of modifiability, a number of tests were made with stimulants and depressants, the general effects of which are known on the system of higher and to a certain extent lower organisms. The results secured shed some light on the processes involved in normal fatigue in the leech, and are consequently given in some detail.

1. General Methods

With the various substances used the necessary strength to be effective was determined by adding a drop at a time of a known strength of solution to the water of a definite volume in a glass dish, the stimulating effects being closely observed. With this known, for convenience and accuracy measurement was then expressed in terms of cubic centimeters. A leech was placed in a freshly made solution and upon coming to attach itself to the bottom of the dish was stimulated posteriorly, the response given representing the first interval recorded. A stop watch was used in timing the duration of the swimming response. The specimens were stimulated until the animal showed no further progressive movement. Upon reaching this condition the leech was

placed in fresh tap water and allowed to revive. This it did in every case except following magnesium sulphate, which for some reason, though slowest of action, seemed to produce the most disastrous results. The necessity of dermic penetration in all of the substances used made the process sometimes a bit prolonged, but the effect of most of the substances was immediately apparent. In no case was the contact stimulus applied sufficient to injure appreciably the animal on which the experiment was being performed.

2. Strychnine

The effect of strychnine is at first to produce a heightened tonus of the nervous system, accompanied by an increased reflex irritability. In this condition a slight contact stimulus is sufficient to cause marked movement, accompanied by tremor or involuntary twitchings of the muscle. The terminations of the motor nerves are paralyzed by large doses. The enormous activity of the muscles produced as the result of strychnine stimulation increases very greatly the consumption of oxygen and the consequent output of carbonic acid, thereby influencing to a great extent the metabolic condition of the animal (Cushny, 1910).

In the experiments on leeches the strength of strychnine found best to employ was a 0.0322 per cent solution. The accompanying table (see table VIII) and the curve of activity (see fig. 8) plotted from the data in this indicate the general effect produced by strychnine on the leech. The features of the response to strychnine in *Dina microstoma* are very much the same as recorded by other investigators for the higher animals. Almost immediately upon being placed in the solution the leech will respond with marked swimming movements to even a slight contact stimulus of the posterior end. In many instances the animals show reactions such as quick jerks, driving the body irregularly through the water. This type of response affords a very clear example of the heightened reflex irritability. Within fifteen minutes to a half hour, varying with the individual, the muscles of the specimen become almost entirely relaxed so that

the animal is scarcely able to respond to the stimulus by even so much as local contraction of the area affected. At this stage the leech becomes so flaccid that it can be removed from the dish over a needle, much as might be done with a piece of ribbon. Within a couple of hours after removal of the specimen to a dish of clean water the poisons have so far dissolved from the system that the animal can perform slow co-ordinated swimming movements in response to stimulation of the posterior end. By the next day it has recuperated to the extent that its responses appear normal.

3. Nicotine

Cushny (1910) says with regard to the effect of nicotine on the lower organisms: "Nicotine has but little toxic action on the lowest invertebrates, but as the nervous system begins to be differentiated it causes paralysis, and still higher in the scale paralytic action is preceded by a stage of stimulation."

When a leech is placed in a 0.00066 per cent nicotine solution, a much increased responsiveness to stimulation is produced. This fact is very apparent upon comparing the curves of activity (see fig. 9) produced by nicotine and strychnine. The strength of nicotine used incites a much more vigorous activity even than strychnine, depression also being produced more rapidly. A clear gelatinous secretion, apparently of mucin, is produced over the surface of the body upon its introduction into the nicotine solution. This doubtless serves, to a certain extent, as a protective coat for the body. It makes stimulation somewhat more difficult to gauge, but with ten individuals comparing so uniformly in general character of response, the source of error from this cause must be extremely constant, or very slight.

The movements produced by contact stimulation under the influence of nicotine are decidedly more abnormal in character, as well as in duration, than were those due to strychnine. Within a short time after introduction into the dish the portion of the body anterior to the clitellum became closely constricted. This contraction of the circular muscles later extended to the posterior regions of the body. Finally paralysis ensues, and the animal becomes incapable of progressive movement. If the leech

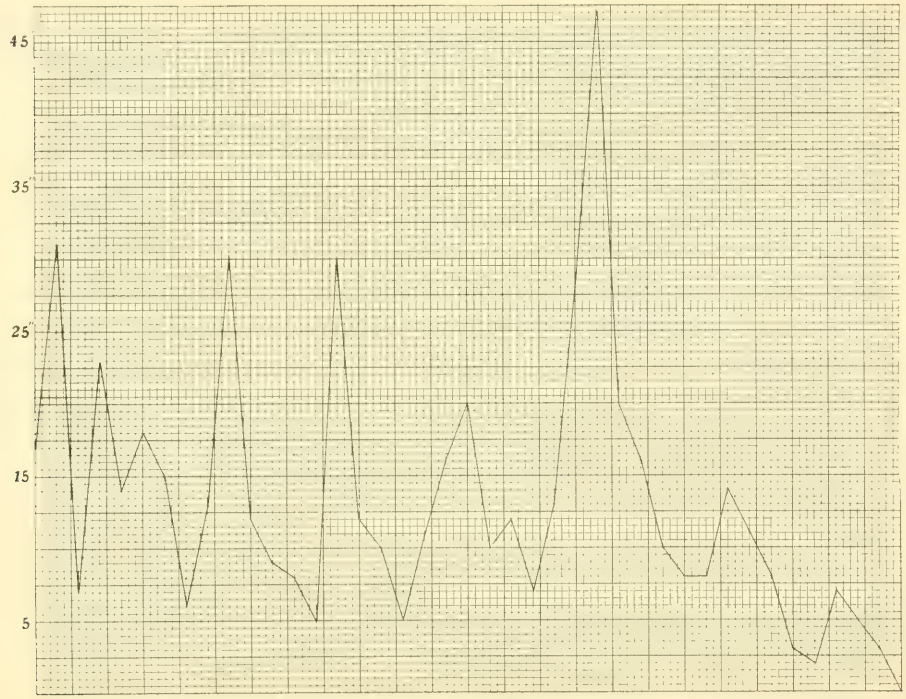


Fig. 8.—Influence of strychnine on curve of activity in the leech. Scale same as in preceding figure. Plotted from record of individual 4, Table 8.

TABLE VIII

Influence of Strychnine Upon the Duration of the Swimming Responses Evoked by Repeated Contact Stimulation

Order of stimulation	Duration in seconds of swimming response in ten specimens of *Dina microstoma*										Average
	1	2	3	4	5	6	7	8	9	10	
1	6	17	15	17	10	25	7	17	10	10	13.4
2	13	13	3	31	22	20	10	8	20	17	15.7
3	7	7	16	7	6	30	6	12	22	21	13.4
4	15	5	8	23	14	15	27	10	8	14	13.9
5	7	12	10	14	9	17	11	45	3	5	13.3
6	16	14	3	18	5	10	9	14	6	10	9.5
7	15	8	14	15	11	7	7	7	9	11	10.4
8	5	10	8	6	8	22	4	6	5	14	8.8
9	16	25	12	13	12	7	3	15	14	8	12.5
10	8	10	11	30	3	8	7	9	14	39	13.9
11	8	10	8	12	6	5	31	10	13	13	11.6
12	7	8	4	9	8	8	29	10	8	21	11.2
13	8	10	4	8	3	4	47	23	3	12	12.2
14	7	11	8	5	2	8	20	5	6	12	8.4
15	7	15	4	30	6	7	23	8	19	13	13.2
16	3	5	8	12	4	6	14	5	5	7	6.9
17	4	10	4	10	0	5	3	8	9	3	5.6
18	3	30	24	5	....	0	8	21	5	2	9.9
19	0	10	7	11	....	....	5	10	3	6	5.3
20	....	8	8	16	....	....	1	23	7	3	6.6
21	....	18	8	20	....	....	0	8	22	0	7.6
22	....	21	8	10	....	....	....	6	13	....	6
23	....	11	15	12	....	....	....	30	8	....	7.6
24	....	9	14	7	....	....	....	4	10	....	4.4
25	....	13	15	13	....	....	....	9	6	....	5.6
26	....	7	8	28	....	....	....	6	9	....	5.4
27	....	8	13	47	....	....	....	0	4	....	7.2
28	....	6	17	20	....	....	....	....	0	....	4.3
29	....	6	3	16	....	....	....	....	....	....	2.5
30	....	4	40	10	....	....	....	....	....	....	5.4
21	....	18	8	20	....	....	0	8	22	0	7.6
32	....	....	15	8	....	....	....	....	....	....	2.3
33	....	....	20	14	....	....	....	....	....	....	3.4
34	....	....	50	11	....	....	....	....	....	....	6.1
35	....	....	16	8	....	....	....	....	....	....	2.4
36	....	....	17	3	....	....	....	....	....	....	2
37	....	....	20	2	....	....	....	....	....	....	2.2
38	....	....	12	7	....	....	....	....	....	....	1.9
39	....	....	0	5	....	....	....	....	....	....	0.5
40	....	....	....	3	....	....	....	....	....	....	0.3
41	....	....	....	0	....	....	....	....	....	....	0

Fig. 9.—Influence of nicotine on curve of activity in the leech. Solid line represents response of individual 7, table IX; dotted line, the average of ten specimens. Scale: five spaces on abscissa represent a single stimulation period; one space on ordinate, two seconds' duration of swimming response.

is immediately removed to a dish of clean water two to four hours serve to remove the nicotine sufficiently for the animals to execute slow but co-ordinated movements. There is considerable variation in this regard, however, since many of the leeches fail to recover entirely from the effects of the nicotine.

TABLE IX

Influence of Nicotine Upon the Duration of the Swimming Responses Evoked by Repeated Contact Stimulation

Order of stimulation	Duration in seconds of swimming response in ten specimens of *Dina microstoma*										
	1	2	3	4	5	6	7	8	9	10	Average
1	9	5	45	20	10	7	15	38	6	5	16
2	5	15	16	12	14	9	19	4	15	3	11.2
3	3	8	6	8	15	21	12	12	22	10	12
4	13	22	13	57	32	17	16	9	12	11	19.2
5	25	12	9	220	246	16	30	22	130	3	71.3
6	19	80	5	13	12	90	34	6	52	22	32.3
7	12	11	54	0	8	10	13	5	20	7	14
8	3	265	9	....	0	140	220	8	8	4	65.7
9	182	20	292	....	....	15	56	330	9	210	111.4
10	28	175	10	....	....	6	10	31	8	15	28.3
11	8	65	0	....	....	0	40	20	23	0	15.6
12	4	17	....	....	....	....	14	0	10	....	4.5
13	5	7	....	....	....	....	12	....	8	....	3.2
14	0	12	....	....	....	....	10	....	14	....	3.6
15	....	8	....	....	....	....	4	....	6	....	1.8
16	....	10	....	....	....	....	0	....	0	....	1
17	....	18	....	....	....	....	....	....	....	....	1.8
18	....	8	....	....	....	....	....	....	....	....	0.8
19	....	6	....	....	....	....	....	....	....	....	0.6
20	....	0	....	....	....	....	....	....	....	....	0

4. Cocaine

With regard to the action of cocaine in invertebrates, Cushny (1910) says: "In some cases, notably in the higher invertebrates, the final depression is preceded by a stage of increased movement, and it is said that irritability of the nerve is also augmented at first." This certainly seems to be the case in *Dina;* for here the activity is at first extremely accentuated, and depression as abrupt. The final effect of the drug seemed to be that of paralysis, the longitudinal muscles often contracting until the body of the animal was very strongly curled. From this

position no degree of stimulation was sufficient to cause straightening out of the body or progressive movement. The strength of cocaine used in these experiments was 0.08 per cent solution. The table showing duration of response (see table X) and the graph (see fig. 10) indicating the same show very clearly the character of the response. Depression was speedy and practically absolute. All of the animals recovered upon being kept in clean water for several hours.

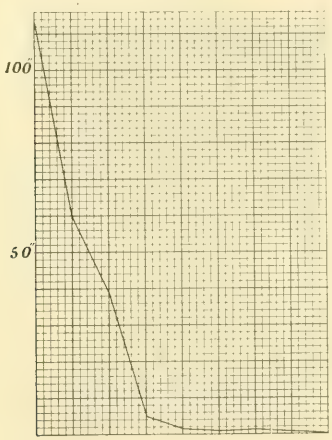


Fig. 10.—Influence of cocaine on curve of activity in the leech. Plotted from average responses of ten leeches. Scale same as in preceding figure.

5. Chloretone

Chloretone was tried and found to be very similar to cocaine in its effects. The initial period of excited responsiveness was even more marked than in the case of cocaine. The following table (see table XI) very clearly indicates this fact. Complete and rapid depression occurred as the result of the poison and the excessive activity of the animal. With a 0.05 per cent solution of chloretone full relaxation of the muscles was secured

in most cases within fifteen or twenty minutes. Upon removal to clean water the leeches within two or three hours recovered sufficiently to perform slow but co-ordinated movements.

6. Magnesium Sulphate

According to Cushny (1910), the magnesium salts have a very powerful action when injected into the higher animals either hypodermically or intravenously. The most characteristic effect is complete anesthesia resembling that induced by the chloroform group and ending in fatal cases in paralysis of the respiratory center.

A strength of magnesium sulphate as high as N ¾ required a rather long period to produce complete depression. In from one to one and a half hours this had occurred. As can be seen from the accompanying table (see table XII), there is at first an increasing excitement, this being followed by a correspondingly slow depression. To a certain extent, at least, paralysis seems to take place in the muscles, a knotted twisting of the body occurring. Later this was followed by relaxation, no response other than a slight lateral movement of the anterior end occurring even to very strong stimulation. This treatment seems to have been more fatal than any of the other substances tried; since out of four individuals tested only one revived to any extent in twenty-four hours, and this not to a stage where co-ordinated movements could take place.

TABLE X

Influence of Cocaine Upon the Duration of the Swimming Responses Evoked by Repeated Contact Stimulation

Order of stimulation	Duration in seconds of swimming response in ten specimens of *Dina microstoma*										
	1	2	3	4	5	6	7	8	9	10	Average
1	18	25	138	215	190	150	185	200	6	10	113.7
2	265	12	4	6	15	5	4	50	230	9	60
3	7	125	2	4	5	3	6	7	10	222	38.6
4	0	5	6	3	2	1	2	6	5	15	4.5
5	....	2	7	1	0	0	1	1	2	2	1.6
6	....	3	2	2	....	....	0	0	0	0	0.7
7	....	1	7	0	....	....	....	....	....	....	0.8
8	....	0	2	....	....	....	....	....	....	....	0.2
9	....	....	0	....	....	....	....	....	....	....	0

Fig. 11.—Influence of magnesium sulphate on curve of activity in the leech. Plotted from record of individual 1, table XII. Scale same as in preceding figure.

TABLE XI

Influence of Chloretone Upon the Duration of Swimming Responses Evoked by Repeated Contact Stimulation

Order of stimulation	Duration in seconds of swimming response in five leeches					
	1	2	3	4	5	Average
1	180	265	360	334	385	304.8
2	30	28	20	20	30	25.6
3	18	5	18	8	90	28.0
4	10	0	10	25	16	12.2
5	3	....	4	18	12	7.4
6	0	....	0	7	5	2.2
7	....	....	....	0	0	0

7. Carbon Dioxide

It is known that oxidation and destruction of carbohydrate in the body result in the formation of at least two waste substances, both of an acid character, namely, carbon dioxide and lactic acid. These two products of metabolism are considered important factors in causing fatigue in skeletal muscle. For them Lee (1910) has suggested the term "fatigue substances." This investigator (1907) found in the frog that upon injecting a 0.07 per cent sodium chloride solution containing considerable quantities of carbon dioxide into the muscles of the leg "it will be observed that the curves of the muscle under the influence of carbon dioxide, from the 1st to the 151st contraction inclusive, are higher than those of the normal muscle,—in other words, carbon dioxide exerts at first an augmenting action. From the two hundred and first contraction on the fatiguing effect is manifest."

A leech placed in 100 cm. of tap water + 100 cm. of carbonated water was at first excited to marked activity. Within five minutes the animal showed depression to the extent that it was incapable of progressive movement. The specimen was immediately removed to a dish of fresh water. It at once began movements of the anterior end, and five minutes later performed swimming movements of a partially co-ordinated character. This was at ten o'clock, and seven minutes after the animal swam actively about in the dish upon being stimulated, though displaying a condition of lower tonus. At twenty minutes past ten the leech appeared entirely normal in its responsiveness.

TABLE XII

INFLUENCE OF MAGNESIUM SULPHATE UPON THE DURATION IN SECONDS OF SWIMMING RESPONSES EVOKED BY REPEATED CONTACT STIMULATION

Order of stimulation	No. of leech 1	No. of leech 2	Average duration	Order of stimulation	No. of leech 1	No. of leech 2	Average duration
1	10	5	7.5	27	15	20	17.5
2	8	8	8	28	0	14	7
3	12	8	10	29	....	40	20
4	6	14	10	30	....	110	55
5	8	7	7.5	31	....	215	107.5
6	7	42	24.5	32	....	25	12.5
7	4	15	9.5	33	....	22	11
8	13	9	11	34	....	7	3.5
9	55	6	30.5	35	....	6	3
10	36	6	21	36	....	5	2.5
11	35	5	20	37	....	12	6
12	14	7	10.5	38	....	10	5
13	30	20	25	39	....	5	2.5
14	18	32	25	40	....	8	4
15	28	12	20	41	....	3	1.5
16	31	7	19	42	....	5	2.5
17	70	8	39	43	....	4	2
18	10	20	15	44	....	2	1
19	35	8	21.5	45	....	3	1.5
20	6	11	8.5	46	....	7	3.5
21	57	16	35.5	47	....	3	1.5
22	66	8	37	48	....	2	1
23	54	25	39.5	49	....	3	1.5
24	179	340	259.5	50	....	2	1
25	21	130	75.5	51	....	0	0
26	45	62	53.5				

Much the same result was secured upon placing leeches in water through which a vigorous stream of carbon dioxide gas had been passed for about twenty minutes. Thus in leeches carbon dioxide is at first accelerating in its action. Depression of the leech comes quickly, but recovery takes place in a relatively short time.

8. MONO-POTASSIUM PHOSPHATE

This substance has been found to be one of the group producing fatigue in skeletal muscle. The experiments of Lee (1907) on the leg muscle of the cat show that at the beginning of the test the contractions of the phosphate muscle were much

greater than those of the normal muscle. After one hundred and seven contractions the phosphate muscle began to show signs of depression.

Leeches placed in a one-seventh gram molecular solution of mono-potassium phosphate (KH_2PO_4) showed signs of considerable excitation extending over some length of time. Within three hours the most of the leeches were in a condition near complete depression. The muscles of the animal appeared flaccid, showing no signs of paralysis. Recovery took place rather slowly as compared with that following the use of carbon dioxide. Within three to four hours after removal to clear water the leeches were usually able to perform well co-ordinated movements, though at a rather slow rate. By the next morning the leeches had practically entirely recovered normal responsiveness.

9. Lactic Acid

Leeches placed in a 0.08 per cent solution of lactic acid (sp. gr. 1.21) required eight or more hours for depression to occur as the result of the solution. With a 0.2 per cent solution this result was secured in a much shorter period. Augmentation of activity upon stimulation seemed to be marked almost to the time of depression. In fact the action of lactic acid on leeches was rather different from that of carbon dioxide and mono-potassium phosphate. A much longer time was required for depression to occur; and when the animal reached this stage the substance had so injured the animal as to prevent its recovery. Whether this is due to the difference between lactic acid and paralactic acid was not made the subject of investigation. Richter (1899), however, states that in all its transpositions paralactic acid behaves like ordinary lactic acid, and hence the same chemical structure is accepted for it. The existence of the two modifications is explained by him as due to the asymmetry of a carbon atom in the acid.

10. Discussion of Fatigue

Fatigue represents a distinct physiological state in an animal. This state carries with it a more or less characteristic type of response in the leech, and very materially influences its degree

of responsiveness. From the experiments discussed in the several preceding pages, it becomes clear that the *modus operandi* of this fatigue is not essentially different from that known in the higher animals. The various depressants used act upon the leech in a manner fundamentally very similar to their action upon vertebrate types. Carbon dioxide, mono-potassium phosphate, and lactic acid have been found in the fatigued muscle of the higher forms, and when applied to these artificially produce a condition of depression. While the analysis of fatigued leech muscle has not been made, I have found that these same substances produce a condition of fatigue in this form. It appears very likely to the writer that in the action of these "fatigue substances" is to be found the explanation of many of the "states of excitement" discussed in a preceding portion of this paper. Such results as those secured from the various substances used on leeches lead one to extend to the lower organisms the following conclusions of Lee (1907): "The facts here reported seem to emphasize anew and strikingly the great desirableness of a very careful and full investigation of the physiological actions on cells, tissues, and organs of the products of metabolism, both intermediate and final products. We seem not yet to realize how potent may be the influence of such substances. We incur the charge of being unscientific if without experimental data we deny to even the humblest katabolic product a possible role as a physiological reagent. It seems to me that physiology is destined to make great progress along the lines here indicated." Such a viewpoint as this is certainly suggestive in its bearing upon the future work in the field of animal behavior.

VI. EFFECT OF COMBINED STIMULI

1. Influence of Food Juices on Reaction to Contact

(*a*) *Normal Individuals.*—Often when a delicate glass rod is brought gently alongside the extreme anterior end of the leech the animal responds by inclining its anterior end in the direction of the stimulus and momentarily attaching the anterior sucker. An immediate recoil is produced, yet nevertheless a positive reaction is involved, the adaptiveness of which has been

considered previously in its relation to the feeding responses of the animal. In studying the feeding reactions of the leech, it was observed that these positive responses seemed to be accentuated under the stimulating influence of the juices of a snail, its favorite food. This point was made the subject of a series of experiments on leeches in normal, starved, and well-fed conditions.

Specimens which had been in the laboratory for a few days only were considered normal. One at the time, a half dozen of these normal leeches were tested for the number of positive responses to thirty very light contact stimuli of the anterior end in the manner above described. After the responses of a particular leech were thus secured in tap water, a considerable quantity of juices extracted by macerating a *Limnea* was added to the water in the dish. The number of positive responses to light contact stimuli was determined under these conditions. The results are indicated in the accompanying table (see table XIII). By positive (+) response is meant the actual application of the anterior sucker against the glass rod as a direct result of the stimulus; negative (—) indicates a direct turn away from the stimulus; and indifferent (±) is a response such as local contraction or a continued forward movement. The uniformity of the results in the different individuals is rather striking. The accentuation of the positive response under the influence of diffusing snail juices is not great, but the increased amount of indifference seems significant. This condition, while apparently

TABLE XIII

Influence of Snail Juice Upon Reactions of Normal Individuals to Contact Stimuli.—Thirty Applications of Stimulus

Number of individual	In fresh tap water			In strong diffusion of snail juice		
	+	—	±	+	—	±
1	13	14	3	13	8	9
2	9	14	7	12	6	12
3	12	13	5	12	6	12
4	5	17	8	8	7	15
5	8	16	6	12	6	12
6	13	14	3	14	6	10
Average	10	14.6	5.4	12	6.5	11.5

non-adaptive, is indirectly of very decided advantage. The increased activity upon which the intensified indifference is dependent serves to bring the animal in contact with a wider field. Its anterior end must necessarily come in touch with the surface upon which it frequently comes to rest from swimming. Thus with the increased number of attachments there would be an increased likelihood of its successfully locating such food as might be in its immediate environment.

(*b*) *Starved leeches.*—Five leeches which had been starved for forty-five days were subjected to a similar treatment to that just described for the normal leeches. The accompanying table (see table XIV) indicates the results secured. The predominance of the negative response of the starved leeches in clean water is to be attributed to the increased irritability of the starved individuals over that in the normal specimens. There is a striking increase of the positive responses, and a considerable difference in the number of indifferent responses under the influence of the snail juice, both of which conditions serve to reduce the number of negative responses in a striking degree.

A comparison of the results secured from the starved individuals with those from the normal individuals affords a good illustration of how the same external factor may affect two organisms in different physiological states. It also serves to show that the juices of the snail reinforce the tendencies toward positive reaction to contact much more in the starved individual than in the normal. It is scarcely necessary to emphasize the adaptive nature of this difference in behavior.

TABLE XIV

Influence of Snail Juice Upon Reactions to Contact Stimuli in Leeches Starved for 45 Days.—Thirty Applications of Stimulus

Number of individual	In fresh tap water			In strong diffusion of snail juice		
	+	−	±	+	−	±
1	11	19	0	19	4	7
2	10	18	2	11	5	14
3	7	19	4	22	3	5
4	9	21	0	19	6	5
5	8	20	2	21	4	5
Average	9	19.4	1.6	18.4	4.4	7.2

TABLE XV

Influence of Snail Juice Upon Reactions of Well-Fed Leeches to Contact Stimulation.—Thirty Applications of Stimulus

Number of individual	In fresh tap water			In strong diffusion of snail juice		
	+	—	±	+	—	±
1	8	18	4	8	7	15
2	10	12	8	9	11	10
3	9	12	9	5	9	16
4	7	19	4	12	6	12
5	5	15	10	10	10	10
6	9	13	8	19	6	5
Average	8	15	7	11	8	11

(*c*) *Well-fed leeches.*—The responses of the well-fed leeches under the same conditions as those of the preceding experiments are not essentially different from what was found to hold in the normal individuals. Under the influence of contact stimulus without the reinforcement of snail juice there is a somewhat smaller number of positive responses than in the normal individual. The same condition is true under the influence of the snail juice. There is, however, a lowered responsiveness in the well-fed individuals which would tend to lower the irritability of the leech. This reduced irritability would tend to render the responsiveness to light contact stimulation more nearly like that of the normal individual which has not previously been excited to a stage of activity.

2. Light and Contact

A dish sixteen by sixteen by thirty-one centimeters containing three dozens of leeches was placed over a 25-watt Mazda light in a dark room, the dish being elevated on a tripod about eight inches in height. With the light turned off a stone was placed in the center of the dish, and underneath this within an hour had accumulated ten of the leeches. The light was then turned on, and the reactions of the leeches were carefully observed. At first the stimulus produced in the leeches under the stone a state of restlessness, indicated by side to side movements. In a few

minutes, however, they became quiet, entirely disregarding the light. The leeches crawling freely about the dish were, however, excited to greater activity, swimming rapidly about in the dish and crawling up its sides. The light seemed to overcome their normal geotactic reactions. Three and a half hours after the beginning of the experiment the animals in contact with the dish and stone were all in the same positions as at first. A half dozen of the others were at rest on the sides of the dish, some of them half out of the water. As many more were swimming about in the dish or crawling on the bottom, while the remainder were massed in clumps on the *Ceratophyllum* in the aquarium, well up towards the top and in the most shaded portion of the dish. Thus, light of the intensity used seems to overcome what geotaxis the leech may have, the orienting effect of its rays tending to carry the animal against the force of gravity. In the case of the leeches underneath the stone, their thigmotactic inclinations being satisfied, light of the intensity used had practically no effect.

Sherrington (1911) says: "It is not usual for the organism to be exposed to the action of only one stimulus at a time. It is more usual for the organism to be acted on by many stimuli concurrently, and to be driven reflexly by some group of stimuli which is at any particular moment prepotent in action on it. Such a group often consists of some one pre-eminent stimulus with others of a harmonious relation reinforcing it." The cases of combined stimuli discussed in the preceding paragraphs afford good examples of how well this principle applies in the leech. In the case of the food juice and contact stimulation, we have a prepotent stimulus in the food, and this reinforces the positive reaction, which represents distinctly one of the feeding reflexes. With light and contact combined, we have a prepotent stimulus in the contact of the animal with the under surface of the stone in the dish. These cases cited in the leech merely indicate the significance of combined stimuli on the behavior of the animal, and point to the fact that behavior represents a resultant action to varied groups of concurrent stimuli.

VII. INFLUENCE OF INTERNAL STATES

1. Behavior of Well-Fed Leeches

Leeches fed to satiety the evening before and left in the dish overnight with an abundant supply of crushed snail for food were tested for the duration of swimming response as evoked by fifteen successive contact stimulations. The comparative curves (see fig. 12) derived from the data given in the following table (see table XVI) show the sluggishness of the well fed individuals as opposed to the responsiveness of the normal specimens. In this condition of satiety the same general dullness of response to stimuli of all kinds is evidenced, as is characteristic of the duration of swimming. The results given in table XVI represent the duration in seconds of the swimming response evoked by posterior end stimulation of comparatively uniform intensity. The average height of the curve of the normal individuals is to be observed as considerably above that of the well fed individuals. The condition of the organism when fed to satiety suggests from the nature of its effect on the responsiveness of the animal a close resemblance to what is secured upon partially fatiguing the individual.

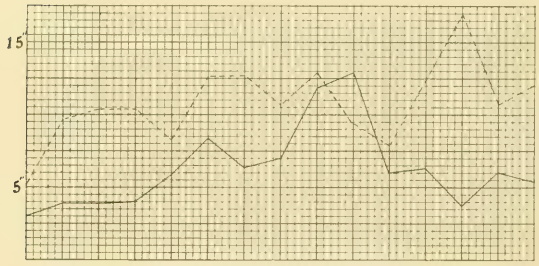


Fig. 12.—Curve showing comparative responsiveness of normal and well-fed individuals to contact stimulation. Dotted line represents responses of normal leeches; solid line, the well fed.

2. Reactions of Starved Leeches

Leeches which had been starved for nearly two months were tested for their general responsiveness. Without the influence of external stimulation they tend to remain quiet for long periods of time even under the influence of a fair amount of illumination. When they are in this quiescent state, often several stimulations of the anterior end are necessary to produce a decided response. Upon their being awakened their response shows an increased irritability over that of the normal specimens, often upon the second or third stimulation the animal responding with a complete recoil and swimming reaction. In this excited condition only a very slight stimulus is necessary to set the leech wildly active again. The starved leech seems to be more easily fatigued upon the application of successive stimuli than is the case with the normal individuals. This is due perhaps to much the same reason as the similar phenomenon in higher animals. Lee (1910) says: "Exact laboratory investigation shows that if most of the carbohydrate be removed from an animal's body, he presents the symptoms of pronounced fatigue;

TABLE XVI

Duration in Seconds of Swimming Response in Normal and Well-Fed Leeches

Order of stimulation	Well fed leeches Number of individual						Normal leeches Number of individual					
	1	2	3	4	5	Average	1	2	3	4	5	Average
1	2	3	3	3	4	3	5	5	5	6	7	5.6
2	2	4	2	6	5	3.8	10	5	13	8	12	9.6
3	4	3	4	4	4	3.8	10	10	8	10	14	10.4
4	8	3	4	2	3	4	12	11	4	10	15	10.4
5	15	4	5	3	2	5.8	8	6	7	9	10	8.2
6	17	5	10	2	8	8.4	7	12	10	25	9	12.6
7	9	3	11	6	3	6.4	4	11	12	21	15	12.6
8	11	2	5	5	12	7	5	8	22	10	8	10.6
9	30	8	8	4	8	11.6	15	12	17	10	10	12.8
10	50	6	3	2	3	12.8	10	5	14	5	13	9.4
11	10	5	6	5	4	6	8	6	8	7	10	7.8
12	10	3	5	6	7	6.2	10	12	18	12	10	12.4
13	3	4	3	5	3	3.6	7	9	35	18	15	16.8
14	5	2	6	4	13	6	10	6	12	15	10	10.6
15	6	3	8	6	4	5.4	15	13	15	8	9	12

and the same is true of his individual muscles, which are incapable of performing as many contractions as the muscles of a normal animal."

As has been stated in the first part of this paper, leeches starved for almost six months show considerable vigor of response. This fact is indicated very clearly by the accompanying curves (see fig. 13) of activity of normal and starved animals. These curves are plotted from forty responses to contact stimulation of the posterior end, and consequently represent only the initial stages of a complete curve of activity. Proportionately the starved specimens show a greater irritability than the normal specimens. The relative nature of the curves seems to indicate that the starved leeches would reach complete depression with a smaller number of stimulations than would the normal specimens.

3. Responses of Undisturbed Leeches

There is in the behavior of the leech a condition corresponding to that of "sleep" in the higher animals. In this state the animal may occupy one of several positions. It may have the anterior eighth of the body turned back over the rest of the body; sometimes it may be coiled slightly; and again, the body may be held entirely straight, the animal hugging the bottom of the dish. In this condition two or more stimuli are necessary to arouse the animal to action. The first stimulus when the leech is in this condition may produce little more than a local contraction; the second, a turn to the left or right as the case may be; while the third will produce a reversal of direction of the anterior end together with swimming. This type of response is just what would be expected in summation effects of stimulation, and this is doubtless the true explanation for the behavior. When the animal is awakened the responsiveness is sharp and vigorous. A slight stimulus of the anterior end may produce a reversal of direction of orientation and subsequent swimming. This would indicate a heightened tonus for the body of the animal as the result of its period of rest, the stimulus liberating a greater supply of energy than normally because of the replenished stores of energy producing material in the tissues of the body.

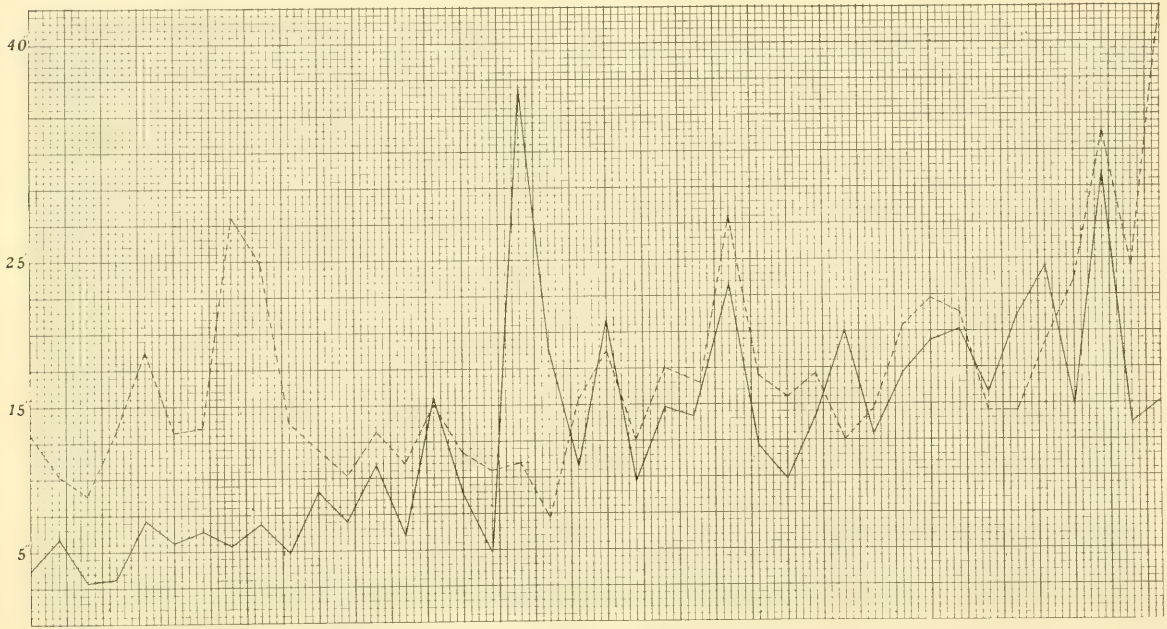


Fig. 13.—Curves showing the comparative responsiveness of normal leeches and leeches starved for six months. Dotted line represents responses of normal leeches; solid line, the behavior of starved leeches.

TABLE XVII

Differences in Seconds in Responsiveness Between Leeches Starved for Approximately Six Months and Normal Individuals

Order of stimulation	Starved specimens							Normal specimens						
	I	II	III	IV	V	VI	Average	I	II	III	IV	V	VI	Average
1	2	2	1.5	4	10	2	3.6	10	42	6	8	4	8	13
2	3.5	1.5	3.5	6	6	16	5.9	16	10	16	6	7	6	10.1
3	1.5	3	2	4	3	3	2.8	13.5	11	6	10	3	10	8.9
4	3.5	3	2	4	3	3	3.1	12	42	11	6	3	6	13.3
5	10	4	1	5	5	18	7.1	17	65	16	5	4	5	18.7
6	5	6	2.5	5	4	11	5.6	10	22	20	11	5	11	13.2
7	2	2.5	1.5	9	8	15	6.3	16	20	16	13	3	13	13.5
8	2.5	9	2	7	4	7	5.3	8	119	17	9	6	9	28
9	6.5	3	3.5	5	16	7	6.8	13	93	18	4	17	4	24.8
10	4.5	4	2	3	9	6	4.8	4	6	8	26	13	26	13.8
11	13.5	13	2.5	9	5	15	9	12	13	15	11	10	11	12
12	7	6	3	8.5	5	13	7	8	14	15	9	6	9	10.1
13	38	4	1.5	3	7	12	10.9	9	11	13	11	24	11	13.2
14	3	5	2.5	4	8	14	6	14	17	14	7	7	7	11
15	52	6	5	5	16	9	15.3	16	11	14	20	9	20	15
16	24	3	3.5	12	5	6	8.9	12	3	16	15	9	15	11.7
17	2	5	3	8	6	5	4.8	4	16	10	13	7	13	10.5
18	197	3.5	2	6	4	7	36.6	10	16.5	14	9	8	9	11
19	84	1	2.5	7	7	10	18.6	8	13	9	5	3	5	7.2
20	27	2	3	4	14	14	10.7	25	20	25	8	5	8	15.2
21	88	6	4	8	16	3	20.8	17	45	21	11	7	11	18.6
22	24	3	6	10	7	8	9.7	24	9	10	12	8	12	12.5
23	28	11	5	8	14	23	14.8	41	14	18	10	6	10	17.3
24	34	3	4	7	18	19	14.1	19	25	28	12	3	12	16.5
25	74	4	5.5	15	21	20	23.3	19	22	88	13	13	13	28
26	36	3	3	5	13	13	12.1	13	13	30	15	16	15	17
27	24	3	9	14	5	4	9.8	19	12	27	16	3	16	15.5
28	53	4	3	11	9	5	14.1	26	8	21	18	12	18	17.1
29	38	9	3	15	47	8	20	17	15	19	7	10	7	12.5
30	33	13	7	8	11	5	12.8	29	11	15	11	11	11	14.7
31	34	8	5	25	8	23	17.1	12	15	55	18	4	18	20.3
32	2	5	2	90	8	9	19.3	50	20	23	12.5	16	12.5	22.3
33	62	19	6	6	14	14	20.1	59	11	16	16	10	16	21.3
34	5	8	5	25	38	13	15.7	33	7	20	11	5	11	14.5
35	41	5	4	57	5	14	21	7	21	22	13	11	13	14.5
36	46	3	5	56	19	18	24.5	20	18	27	11	29	11	19.3
37	39	4	7.5	15	15	8.5	14.8	70	19	10	12	18	12	23.5
38	47	5	4	97	8	24	30.8	120	45	20	3	11	3	33.7
39	27	13	5	6	17	13.5	13.6	74	13	24	11	14	11	24.5
40	3	5	5	55	11	12	15.1	148	44	41	6	10	6	42.5

The general responsiveness of the leeches in normal, starved, and well-fed states indicates the influence that metabolic conditions may have upon the reactions of the animal which has formed the subject for this investigation. The effect of feeding to satiety seems a generally depressing one, perhaps due, as has been shown in the case of fatigue, to substances produced in the body tissues of the animal incident to its digestive processes. In this connection an idea of Lee (1910) is highly suggestive: "It is impossible to avoid a strong suspicion that the presence of a superfluity of foodstuffs within the body leads to an accumulation of intermediate metabolic products which in themselves act on the tissues as fatigue substances." In the starved condition, the animal has remained quiet sufficiently long for the system to have become largely rid of such substances, and at first is somewhat low in responsiveness. As the fatigue substances increase, irritability is increased to the stage where the accumulation of these substances and the depleted stores of energy furnishing materials cause depression to set in.

VIII. GENERAL CONSIDERATIONS ON MODIFIABILITY IN LEECHES

Much stress has been placed in recent years upon the great variability of reactions in organisms. Not only has there been shown in numerous instances marked differences in the behavior of different individuals of a particular species, but there have been demonstrated wide variations in the responses given by the same individual to a particular stimulus at different times. This variability of reaction has been shown to be largely due to internal changes in the animal. Attention has been directed quite properly towards this plastic element in an organism's responsiveness; for the work which has been the outcome of the projection of such a view has served to place the behavior of an animal in its true perspective. Far from projecting the analysis of behavior into the realm of vagueness and mysticism, it has only made more apparent the fact that the problem of this analysis is one much more complex than was formerly supposed.

The most interesting and significant feature in animal behavior is the regulatory nature of the responses. The fact that

a living organism can within certain limits adjust itself to the varying factors in its life-complex is its own peculiar characteristic. Yet even here there is a limit to the element of plasticity; perhaps the moth, unless it changes its physical make-up, will ever be doomed to meet death about an arc-light or a trap lantern. Not all behavior is adaptive in character, and particularly is this true when the animal is placed amid the factors of a new environment. In the words of Wasmann: "Both elements, automatism and plasticity, are found in different proportions with all animals from the highest to the lowest." Modifiability in the behavior of animals, generally, falls into two categories: (1) modifications of reflex responses without the intervention of intelligence, and (2) the intelligent modifications, or those effected through the power of association formation. In the study on leeches presented in this paper, only the first of these types of modifiability has been considered.

The random movements of the leech afford an excellent illustration of the function of modifiability in a lower organism. Illumination of a fair intensity seems to interfere with the normal processes of the leech. When it is subjected to light of 100-watt intensity random movements are the response immediately given by the organism. Through these the leech is enabled to locate finally a region of lower light intensity in another part of the dish. Through the same agency the leech succeeds, after numerous trials, in locating its food, as well as in performing numerous other features of its daily life. In the lower organisms modifiability plays the rôle largely assumed by intelligent action in the higher animals.

The analysis of this modifiability is very largely facilitated through the principles already demonstrated in the higher animals by such able workers as Sherrington (1911), Lee (1907, 1910), and numerous others. Whatever merit this paper on leeches may have is due, in the opinion of the writer, to the fact that its chief attempt has been to determine to what extent these principles are manifested in the behavior of the leech. While no one can be more fully aware than the writer of the imperfection of the methods employed in many of the experiments and the inadequacy of the data presented in support of certain con-

clusions, still the aim throughout the second part of this paper has been to present, so far as possible, a causal explanation of the behavior described.

The different responses to the same stimulus have been shown in their essential features to be in accord with our knowledge of reflex-arc structure and what might be expected of its conductivity in the various stages of excitement of the leech. Acclimatization to slight stimuli has been explained on the basis of the dulled sensibility of the receptors and slight changes in the nerve centers involved. It has been shown that the phenomenon of fatigue in the leech possesses the same fundamental characteristics as fatigue in skeletal muscle. An important factor in explaining the behavior of the organism at a given moment has been shown to be the consideration of the concurrent stimuli operative at that moment. Perhaps intermediate metabolic products are the cause of much of the difference in responsiveness between normal and well fed leeches. The increased irritability of starved leeches is likely due to much the same cause.

The stage has been reached in the investigation of animal behavior where vague generalizations cease to be of value. The most urgent need of the science is a deliberate and extended study of the component factors of the physiological states so profoundly modifying the character of reaction to a given stimulus. Each animal, as well as each group of animals, possesses its own characteristic types of reaction, which demand for their proper understanding a careful physiological analysis.

IX. SUMMARY

A. The General Reactions of the Leeches *Dina microstoma* Moore and *Glossiphonia stagnalis* Linnaeus

1. The most abundant species of leeches occurring in the vicinity of Berkeley appear to be *Glossiphonia stagnalis* Linnaeus and *Dina microstoma* Moore. It was upon these two kinds of leeches that the major portion of the work embodied in this paper was performed.

2. The chief interest manifested in the literature on the reactions of leeches has been centered in the blood-leech because of its former important relation to medicine.

3. Random movements or the tendency to "prove all things, hold fast that which is good," constitute perhaps the most significant single feature of leech behavior.

4. *Dina microstoma* moves forward by the looping or the swimming type of response. *Glossiphonia stagnalis* and *Hemiclepsis occidentalis* Verrill have their body structure modified for carrying their young. It is perhaps for this reason that they do not possess the swimming type of locomotion.

5. Rhythmical undulatory movements in leeches seem to perform a respiratory function. Perhaps to a certain extent they also exercise an accessory excretory function.

6. There is a marked tendency for the leeches *Glossiphonia stagnalis* and *Dina microstoma* to collect in groups. The determining factors in this group formation are the thigmotactic propensities and negative phototaxis.

7. To a large extent *Dina microstoma* appears to be a scavenger; for it feeds upon dead fish, crushed snails (*Limnea, Physa, Planorbis*), recently killed crayfish, and similar food. *Glossiphonia stagnalis* was kept in good condition by feeding it small living earthworms.

8. Leeches are very sensitive, showing marked responses to various light stimuli. Care must be exercised if such behavior is to be observed.

9. Both *Dina microstoma* and *Glossiphonia stagnalis* are negatively phototactic. A strong light intensity produces a greater initial number of random movements than does a low candle power light, and appears to exert a more decided orienting effect.

10. The nephelid is positively rheotatic. This reaction serves to keep it in its breeding locality.

11. To localized injurious chemical stimuli *Dina microstoma* shows a decided negative response. The diffusing juices of a snail produce a positive reaction.

12. Super-optimum temperatures produce a greater degree of activity, accompanied by an accentuation of the tendency to perform random movements.

13. Positive thigmotaxis is shown in the collections of leeches underneath stones, in their reactions to food, and to a certain degree to slight contact stimuli. Negative reactions are given to localized contact, heat, and chemical stimuli.

14. *Glossiphonia* and *Dina* are able to undergo successfully only a very slight degree of desiccation.

15. *Glossiphonia stagnalis* and *Dina microstoma* are hermaphroditic, fertilization taking place by means of a hypodermal impregnation with spermatophores. *Dina* lays its eggs in a cocoon after the manner of the earthworm. The eggs of *G. stagnalis* are carried attached to the ventral surface of the body, as are also the young upon hatching.

16. In the behavior of *G. stagnalis*, no presence of an "incubation instinct" seems to be evidenced. The adults show no signs of a "parental" instinct; they carry their young only because the small leeches are very persistently and strongly thigmotactic.

17. Both *Glossiphonia* and *Dina* are active mainly at night, and during the day remain underneath stones or in the less lighted portions of the aquaria.

18. The young of *Glossiphonia stagnalis* exhibit behavior essentially the same as that of the adults. The chief difference is the intensified positive thigmotaxis of the juvenile forms.

19. The chief function of the brain in the leech appears to be production of spontaneity of movement. There is in the decapitated specimens a marked decrease in the number of internally initiated movements.

B. Modifiability in the Behavior of the Leech *Dina microstoma* Moore

20. The behavior of the leech is eminently modifiable, the reaction at any one moment representing the resultant of many concurrent stimuli, internal as well as external.

21. Contact stimulation of the anterior end, of relatively uniform intensity and applied to a particular part, produces several different types of response. The determining factors in this variable behavior in the leech appear to be the intensity and localization of the stimulus, since these can be only approximately regulated, the position of the body at the time of stimulation, the tonus of the organism, and the sequence of the reaction in the chain reflex involved.

22. The leech acclimatizes readily to slight shocks and shadows repeated at thirty-second intervals. This acclimatization does

not seem to be due to muscular fatigue, but to either a dulling of the sensibility of the receptors or to slight changes in the nerve centers concerned, or perhaps both of these latter factors may be involved.

23. Repeated contact stimulation of the posterior end induces at first a gradual increase in activity followed by a gradual decrease, concluding with complete depression.

24. The effects of strychnine, nicotine, cocaine, chloretone, and magnesium sulphate on the leech appear in their fundamental characteristics the same as those produced in the higher animals.

25. Carbon dioxide, mono-potassium phosphate, and lactic acid, the substances probably causing fatigue in the higher animals, are found experimentally to produce at first a much increased activity in the leech, followed by a complete depression. This parallelism in the effects of these substances suggest that they are very likely contributory to the production of fatigue in the leech.

26. The presence of diffusing food juices intensifies the tendency to positive reaction to light contact stimulation. This is particularly the case in the starved leech. Thigmotactic proclivities very materially affect, at times, the reactions of the animal to light.

27. The internal states of the leech exercise a profound influence upon its behavior. The chief effect of hunger and satiety seems to be that of altering the irritability of the animal; hunger producing a greater relative responsiveness; satiety, a tendency towards sluggishness. It is suggested that the presence of a superfluity of foodstuffs within the body leads to the accumulation of intermediate metabolic products which may react on the animal as do the fatigue substances.

28. The attempt in this paper on the modifiability of behavior in the leech has been to analyze, so far as possible, this behavior into its component physiological factors. In the opinion of the writer, such a method should lead to the kind of results most needed in the science of animal behavior.

X. BIBLIOGRAPHY

Adams, G. P.

1903. On the negative and positive phototropism of the earthworm, *Allolobophora foetida* (Sav.), as determined by light of different intensities. Amer. Journ. Physiol., **9**, 26–34, 2 figs. in text.

Allee, W. C.

1912. An experimental analysis of the relation between physiological states and rheotaxis in Isopoda. Journ. Exp. Zool., **13**, 269-344, 10 figs. in text.

Apathy, S.

1888. Süsswasser Hirudineen. Zool. Jahrb. Syst., **3**, 725–794.

Beddard, F. E.

1896. "Hirudinea," *in* Cambr. Nat. Hist. (New York, Macmillan Co.), 2, 392–408, 257 figs. in text.

Biedermann, W.

1910. "Die Aufnahme, Verarbeitung und Assimilation der Nahrung, IV, Die Anneliden," *in* H. Winterstein's Handbuch der Vergleichenden Physiol. (Jena, Gustav Fischer), 1 and 2, pp. 540–602, 26 figs. in text.

Bohn, G.

1907. Les tropismes, la sensibilité différentielle et les associations chez le Branchellion de la torpille. C.-R. Soc. Biol., Paris, **63**, 545–548, 1 fig. in text.

1909a. Sensibilisation et désensibilisation des corallaires fouisseurs. *Ibid.*, **67**, 484–486, 1 fig. in text.

1909b. La sensibilisation et la desensibilisation, considérées du point de vue de la chemie physique. *Ibid.*, **67**, 542–544, 1 fig. in text.

1909c. Sensibilisation et désensibilisation dues a des excitations répétées. *Ibid.*, **67**, 634–636, 1 fig. in text.

1909d. La naissance de l'intelligence. (Paris, E. Flammarion), 350 pages, 40 figs. in text.

Bolsius, H.

1911. Notice sur la biologie des Clepsines. Zool. Anz., **38**, 454–455, 1 fig. in text.

Bonnet, S.

1775. Lettre à Valmont de Bomare sur les sangsues considérées, non comme baromètres, mais comme thermomètres. Rozier, Obs. Phys., 5, 170.

Brandt, J. F., and Ratzeburg, J. T. C.

1833. Medizinische Zoologie (Berlin, Trowitzsch und Sohn), 2, iv + 364, 37 plates.

Brumpt, E.

1901. Reproduction des hirudinées. Mém. Soc. Zool. France, **13**, 286-430, 64 figs. in text.

Bristol, C. L.
1898. The metamerism of Nephelis. Journ. Morph., 15, 17–64, 3 figs. in text, 4 pls.

Busquet, Leon
1854. Manuel de hirudiculture, ou de l'elève des sangsues. (Bordeaux, Balarac), 180 pp.

Carlet, G.
1883a. Le mode de fixation des ventouses de la sangsue, étudié per la méthode graphique. C.-R. Acad. Sci., Paris, 96, 448–449.
1883b. Sur la morsure de la sangsue. *Ibid.*, 96, 1244–1246.
1883c. Sur les mécanismes de la succion et de la déglutition chez la sangsue. *Ibid.*, 96, 1439–1440.
1883d. Le procédé opératoire de la sangsue. Rev. Scientif., 32, 210-213.

Castle, W. E.
1900. Some North American fresh-water Rhynchobdellidae and their parasites. Bull. Mus. Comp. Zool. Harv. Coll., 36, 17–64, 4 figs. in text, 8 pls.

Cushny, A. R.
1910. Pharmacology and therapeutics. (Lea Bros. & Co., Philadelphia), 744 pp., 52 figs. in text.

Darwin, C.
1883. The formation of vegetable mould through the action of worms with observations on their habits. (London, John Murray, 1904), viii + 298, 2 figs. in text.

Ebrard, E.
1857. Nouvelle monographie des sangsues médicinales. (Paris, J. B. Baillière et fils), xxiii + 494, 12 pls.

Fermond, C.
1854. Monographie des sangsues médicinales. (Paris, Germier Baillière), 512 pp., 2 pls.

Gee, W., and Lathrop, F. H.
1912. Death-feigning in *Conotrachelus nenuphar* Herbst. Ann. Entomol. Soc. Amer., 5, 391–399, 1 fig. in text.

Gibbs, H.
1897. Notes on *Pontobdella muricata*. Journ. Mar. Biol. Assoc., n. s., 5, 330–332.

Gluschkiewitsch, T. H.
1907. Regenerations des Vorder- und Hinterendes der *Clepsine tessulata*. Arch. Entw. Mech., 25, 1–6, 4 figs. in text.

Graf, A.
1899. Hirudineenstudien. Nova Acta Ac. Caes. Leop. Carol., 72, 217-403, 15 pls.

Grube, A. E.
1844. Untersuchungen über die Entwicklung der Clepsine. (Königsberg, Gebr. Bornträger), vi + 56, 3 pls.

Harding, W. A.
1910. A reversion of the British leeches. Parasitology, 3, 130–201, 16 figs. in text, 3 pls.

Hargitt, C. W.
1906. Experiments on the behavior of tubicolous annelids. Journ. Exp. Zool., 3, 295–320, 3 figs. in text.

Harper, E. H.
1905. Reactions to light and mechanical stimulation in the earthworm *Perichaeta bermudensis* (Beddard). Biol. Bull., 10, 17–34, 5 figs. in text.

Hirschler, J.
1907. Ueber regulatorische Vorgänge bei Hirudineen nach dem Verluste des hinteren Körperendes. Zool. Anz., 32, 212–216.

Hoffmeister, W.
1845. Die bis jetzt bekannten Arten aus der Familie der Regenwürmer. (Braunschweig, Vieweg und Sohn), 43 pp., 1 pl.

Holmes, S. J.
1905. The selection of random movements as a factor in phototaxis. Journ. Comp. Neur. and Psych., 15, 98–112.
1907a. Rhythmical activity in Infusoria. Biol. Bull., 13, 306–308.
1907b. The behavior of *Loxophyllum* and its relation to regeneration. Journ. Exp. Zool., 4, 399–418, 7 figs. in text.
1911a. The reactions of mosquitoes to light in different periods of their life-history. Journ. Anim. Behav., 1, 29–32.
1911b. The evolution of animal intelligence. (New York, Henry Holt Company), v + 296, 17 figs. in text.

Houghton, W.
1861. Remarks on the Glossiphonidae, a family of discophorous Annulata. Quart. Journ. Micr. Sci., n. s., 1, 33–39, 1 pl.
1863. Leech-Lore. Intell. Observ., 2, 354–361.

Iijima, I.
1882. Origin and growth of the eggs and egg strings in *Nephelis*. Quart. Journ. Micr. Sci., n. s., 22, 189–211.

Jennings, H. S.
1902. On the behavior of fixed Infusoria (*Stentor* and *Vorticella*), with especial reference to the modifiability of protozoan reactions. Amer. Journ. Physiol., 8, 23–60, 10 figs. in text.
1905. Modifiability in behavior, I. Behavior of sea-anemones. Journ. Exp. Zool., 2, 447–472.
1906a. Factors determining direction and character of movement in the earthworm. Journ. Exp. Zool., 3, 435–455, 1 fig. in text.
1906b. Behavior of the lower organisms. (New York, Macmillan Co.), xiv + 366, 144 figs. in text.

Laurens, A. P.
1854. Mémoire sur l'hirudiniculture, ou l'elève des sangsues, considérées sous le rapport commercial, industriel, agricole, humanitaire et hygienique. (St. Germain en Laye, Beau.)

Lee, F. S.
1907. The cause of the treppe. Amer. Journ. Physiol., 18, 267–282, 2 pls.
1910. The nature of fatigue. Pop. Sci. Month., 76, 182–195, 7 figs. in text.

Loeb, J.
1894. Beiträge zur Gehirnphysiologie der Würmer. Arch. ges. Physiol., 56, 247–269, 4 figs. in text.
Masterman, E. W. G.
1908. Hirudinea as human parasites in Palestine. Parasitology, 1, 182–185.
Moltschanov, L. A.
1911. Ein Beitrag zur Biologie der Clepsinen (Hirudinea). Zool. Anz., 38, 155–158, 3 figs. in text.
Moore, J. Percy
1901. The Hirudinea of Illinois. Bull. Ill. State Lab. Nat. Hist., 5, 479–547, 6 pls.
Moquin-Tandon, A.
1827. Monographie de la famille des Hirudinees. (Montpellier, Jean Martel), 151 pp., 7 pls.
1846. *Idem.* Nouvelle edition revue and augmentée. (Paris, J. B. Baillière), 448 pp., 14 pls.
Morgan, T. H.
1901. Regeneration. (New York, Macmillan Company), xii + 316, 66 figs. in text.
Mosso, Angelo
1904. Fatigue. (New York, Drummonds), xiv + 334, 30 figs. in text.
Nachtrieb, H. F., Moore, J. P., and Hemingway, E. E.
1912. The leeches of Minnesota. Geol. and Nat. Hist. Survey of Minn., Zool. Ser., V, 150 pp., 7 pls.
Parker, G. H.
1901. The directive influence of light on the earthworm, *Allolobophora foetida.* Amer. Journ. Physiol., 5, 151–157, 1 fig. in text.
Pearl, R.
1903. The movements and reactions of fresh-water planarians: a study in animal behavior. Quart. Journ. Micr. Sci., 46, 509-714, 49 figs. in text.
Richter, V. von
1899. Organic Chemistry. (Philadelphia, Blakiston's Son & Co.), 1, xviii + 625.
Riley, C. F. C.
1912. Observations on the ecology of dragon-fly nymphs: reactions to light and contact. Ann. Entomol. Soc. Amer., 5, 272–292.
Severin, H. H. P., and Severin, H. C.
1911. Habits of *Belostoma* (= *Zaitha*) *flumineum* Say and *Nepa apiculata* Uhler, with observations on other closely allied aquatic hempitera. Journ. N. Y. Entom. Soc., 19, 99–108.
Sherrington, C. S.
1906. The integrative action of the nervous system. (New Haven, Yale University Press), xvi + 441, 85 figs. in text.
Smith, Amelia C.
1902. The influence of temperatures, odors, light, and contact on the movements of the earthworm. Amer. Journ. Physiol., 6, 459–486.

Uexküll, J. von
1905. Studien über den Tonus, III. Die Blutegel. Zeitschr. f. Biol., **46**, 372–402, 17 figs. in text.
1909. Umwelt und Innenwelt der Tiere. (Berlin, Springer), 159 pp.
Valmont de Bomare, J. C.
1776. Article sangsue. Diction. d'Histoire Nat. (Lyon, 3e édition), **8**, p. 63.
Verrill, A. E.
1873. Synopsis of the North American fresh-water leeches. U. S. Fish Com. Rep., 1872–1873, 666–689.
Vitet, L.
1809. Traité de la sangsue médicinale. (Paris), 1 pl.
Wagner, G.
1905. On some movements and reactions of *Hydra*. Quart. Journ. Micr. Sci., **46**, 585–622, 6 figs. in text.
Whitman, C. O.
1878. The embryology of *Clepsine*. Quart. Journ. Micr. Sci., **18**, 215-315, 4 pls.
1886. The leeches of Japan. *Ibid.*, **26**, 317–416, 5 pls.
1891. Spermatophores as a means of hypodermic impregnation. Journ. Morph., **4**, 361–495, 1 pl.
1899. Animal behavior. Biol. Lect. Marine Biol. Lab., Woods Holl, 1898, pp. 285–338.
Yerkes, Ada W.
1906. Modifiability of behavior in *Hydroides dianthus* V. Journ. Comp. Neur. Psychol., **16**, 441–449, 1 fig. in text.
Yerkes, R. M.
1912. The intelligence of earthworms. Journ. Anim. Behav., 5, 332-352, 5 figs. in text.
Yoakum, C. S.
1909. An experimental study of fatigue. Psychol. Monographs, **12**. vi + 131.

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY
Vol. 11, No. 12, pp. 307-328, pls. 13-15 February 21, 1914

THE STRUCTURE OF THE OCELLI OF *POLYORCHIS PENICILLATA*

BY
ETTA VIOLA LITTLE

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY

UNIVERSITY OF CALIFORNIA PUBLICATIONS

Note.—The University of California Publications are offered in exchange for the publications of learned societies and institutions, universities and libraries. Complete lists of all the publications of the University will be sent upon request. For sample copies, lists of publications or other information, address the Manager of the University Press, Berkeley, California, U. S. A. All matter sent in exchange should be addressed to The Exchange Department, University Library, Berkeley, California, U. S. A.

OTTO HARRASSOWITZ, LEIPZIG.

Agent for the series in American Archaeology and Ethnology, Classical Philology, Education, Modern Philology, Philosophy, Psychology, History.

R. FRIEDLAENDER & SOHN, BERLIN.

Agent for the series in American Archaeology and Ethnology, Botany, Geology, Geography, Mathematics, Pathology, Physiology, Zoology, and Memoirs.

ZOOLOGY.—W. E. Ritter and C. A. Kofoid, Editors. Price per volume, $3.50. Commencing with Volume II, this series contains Contributions from the Laboratory of the Marine Biological Association of San Diego.

Cited as Univ. Calif. Publ. Zool.

Volume 1, 1902-1905, 317 pages, with 28 plates $3.50

Volume 2 (Contributions from the Laboratory of the Marine Biological Association of San Diego), 1904-1906, xvii + 382 pages, with 19 plates $3.50

Volume 3, 1906-1907, 383 pages, with 23 plates $3.50

Volume 4, 1907-1908, 400 pages, with 24 plates $3.50

Volume 5, 1908-1910, 440 pages, with 34 plates $3.50

Vol. 6.

1. (XXIII) On the Weight of Developing Eggs. Part I, The Possible Significance of Such Investigations, by William E. Ritter; Part II, Practicability of the Determinations, by Samuel E. Bailey. Pp. 1-10. October, 1908 ..... .10
2. (XXIV) The Leptomedusae of the San Diego Region, by Harry Beal Torrey. Pp. 11-31, with 11 text-figures. February, 1909 ..... .20
3. (XXV) The Ophiurans of the San Diego Region, by J. F. McClendon. Pp. 33-64, plates 1-6. July, 1909 ..... .30
4. (XXVI) *Halocynthia johnsoni* n. sp.: A comprehensive inquiry as to the extent of law and order that prevails in a single animal species, by Wm. E. Ritter. Pp. 65-114, plates 7-14. November, 1909 ..... .50
5. (XXVII) Three Species of *Cerianthus* from Southern California, by H. B. Torrey and F. L. Kleeberger. Pp. 115-125, 4 text-figures. December, 1909 ..... .10
6. The Life History of *Trypanosoma dimorphon* Dutton & Todd, by Edward Hindle. Pp. 127-144, plates 15-17, 1 text-figure. December, 1909 ..... .50
7. (XXVIII) A Quantitative Study of the Development of the Salpa Chain in *Salpa fusiformis-runcinata*, by Myrtle Elizabeth Johnson. Pp. 145-176. March, 1910 ..... .35
8. A Revision of the Genus *Ceratocorys*, Based on Skeletal Morphology, by Charles Atwood Kofoid. Pp. 177-187. May, 1910 ..... .10
9. (XXIX) Preliminary Report on the Hydrographic Work Carried on by the Marine Biological Station of San Diego, by George F. McEwen. Pp. 189-204; text-figure and map. May, 1910 ..... .15
10. (XXX) Biological Studies on *Corymorpha*. III, Regeneration of Hydranth and Holdfast, by Harry Beal Torrey. Pp. 205-221; 16 text-figures.
11. (XXXI) Note on Geotropism in *Corymorpha*, by Harry Beal Torrey. Pp. 223-224; 1 text-figure.
    Nos 10 and 11 in one cover. August, 1910 ..... .20
12. The Cyclostomatous Bryozoa of the West Coast of North America, by Alice Robertson. Pp. 225-284; plates 18-25. December, 1910 ..... .60
13. Significance of White Markings in Birds of the Order Passeriformes, by Henry Chester Tracy. Pp. 285-312. December, 1910 ..... .25
14. (XXXIII) Third Report on the Copepoda of the San Diego Region, by Calvin Olin Esterly. Pp. 313-352; plates 26-32. February, 1911 ..... .40
15. The Genus *Gyrocotyle*, and Its Significance for Problems of Cestode Structure and Phylogeny, by Edna Earl Watson. Pp. 353-468; plates 33-48. June, 1911 ..... 1.00

Index, pp. 469-478.

---

*Roman numbers indicate sequence of the Contributions from the Laboratory of the Marine Biological Association of San Diego.

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY
Vol. 11, No. 12, pp. 307-328, pls. 13-15 February 21, 1914

THE STRUCTURE OF THE OCELLI OF *POLYORCHIS PENICILLATA*

BY
ETTA VIOLA LITTLE

INTRODUCTION

The genus *Polyorchis* was founded by Alexander Agassiz in 1862 (in L. Agassiz, 1862) to include the California species *penicillatum* which Eschscholtz (1829) had described and placed in the genus *Melicertum*. Haeckel (1880) claimed that by right of priority the generic name *Melicertum* should be retained for this species. Lankester (1900) places the genus *Polyorchis* in the family Cannotidae of the Leptomedusae, while Fewkes (1889) placed it among the Anthomedusae. The latter says: "There seems to be no doubt that *Polyorchis* belongs to the true Anthomedusae and that it is closely allied to *Sarsia*, as suggested by rows of meridionally placed nematocysts on the outer wall of the bell." And again, "*Polyorchis* is the largest medusa of tubularian hydroids or Anthomedusae yet found in American waters." Mayer (1910) correctly assigns *Polyorchis* to the Leptomedusae, family Thaumantiadae, without lithocysts, subfamily Polyorchinae, with diverticula on radial canals ending blindly.

Haeckel (1880) divides the genus into three species. *P. pinnatus* is described as being distinguished from *penicillata* by the smaller number of lateral branches of the radial canals and the larger number of gonads and tentacles, there being eight gonads on each of the four radial canals, and forty tentacles of the same length in a single row. On the other hand *P. penicil-*

lata is stated to have but four gonads suspended from each of the four radial canals, and thirty-six tentacles, also equal in size and attached in a single row. The third species given is *P. campanulata.* This form has a much greater number of lateral branches to the radial canal, a large number of tentacles, varying from fifty to one hundred and fifty, arranged in four rows over one another on the rim. These are divided into eight large upper and outer (four radial and four inter-radial); sixteen shorter, within and below the outer; forty-eight still shorter and inner; and fifty to one hundred to numerous, very short, and placed on the extreme lower edge of the rim. Murbach and Shearer (1903) give *P. minuta* as a distinct species, based principally on the size. Our material leads us to regard these three species as growth forms of one species, *P. penicillata.*

The specimens upon which the present studies were made were obtained at different times from December to the middle of April at the Oakland pier, San Francisco Bay.

METHODS

The preparation of slides for the study of the structure of the ocelli presents many difficulties. For his willing help in aiding me in this difficult technique I wish to express my appreciation to Dr. J. A. Long and also to Professor C. A. Kofoid, under whose direction this study was undertaken, for his kindly aid and criticism.

One of the first difficulties encountered is that of infiltration. The animal is of such a jelly-like consistency and contains such a high percentage of water that dehydration without undue hardening becomes a problem. After repeated trials it was found that small pieces of the margin of the bell bearing the bases of the tentacles, from animals fixed in Zenker's or Bouin's fluid and preserved in seventy per cent alcohol, could be satisfactorily dehydrated by leaving them in ninety per cent and then in absolute alcohol for from eight to ten hours each. For infiltration the best results were obtained by transferring the tissue directly from the one hundred per cent alcohol to chloroform, to which

paraffin was then added, and finally into melted paraffin (55° C.) for about fifteen minutes. The sections were cut three, six, or seven microns thick and mounted in the usual way.

Many complications arose in the process of staining, for many of the ordinary dyes produced little or no differentiation. Safranin, carmine, methylen blue, light green, and several other dyes were tried, but with unsatisfactory results. Iron-alum haematoxylin with a number of counter-stains was tried, but these proved of little value. Delafield's haematoxylin with eosin was fairly satisfactory and for the study of pigment was perhaps the best stain of all tried. For a general differentiation, Mallory's connective tissue stain with acid fuchsin gave excellent contrasts, though the cell structures were not so well defined.

The best preparations were obtained with the material fixed in Zenker's or Bouin's fluid and stained with Mallory's phosphotungstic acid haematoxylin, used as follows at room temperature:

Potassium permanganate, 0.2%	8 to 10 minutes.
Oxalic acid, 2%	10 minutes.
Phosphotungstic acid haematoxylin	12 to 14 hours.

The tissue for the above formula should be fixed with Zenker's fluid. If Bouin's is used, the slides should remain for at least twenty minutes in the potassium permanganate.

For maceration preparations the Hertwigs' (1878) plan was followed. The fresh tissue remains in equal parts of 0.05 per cent osmic acid and 0.2 per cent acetic acid for about two minutes, and is then washed several times in 0.1 per cent acetic, in which it then remains for from twelve to twenty-four hours. The eyespots can then be easily teased or shaken loose from the tentacles, mounted in glycerine and Beale's carmine, and disassociated by tapping upon the coverglass.

STRUCTURE

The animal is bell-shaped. The sides are nearly vertical, becoming rounded or almost hemispherical at the aboral end (pl. 13, fig. 1). Fewkes (1889) describes a conical projection or thickening at the top, but of all those specimens examined by me

only a very few had a tendency toward a small apical cone. The bell terminates abruptly with little decrease orally in diameter and is partly closed by the thin velum (*vel.*, pl. 13, figs. 1, 2) which leaves a small opening, about one-third to one-fourth the diameter, in the center. Within the thick jelly-like mass (*mes.*) of the outer bell (*o. w.*) can be seen the outline of a smaller one similar in shape, formed by the lining (*in. w.*) of the bell. In the large adult the outer and inner bell attain a height of 24 mm. and 18 mm. respectively, and a diameter of 22.5 mm. and 17 mm. The smallest specimens observed were 1 by 1 mm. These measurements differ from those of Fewkes, (1889), who gives the dimensions as one and one-half times as high as broad.

The four-lipped manubrium (*man.*) extends from the opening in the velum to an enlarged sac-like stomach at the apex of the inner bell. From this branch the four radial canals (*r. can.*) which extend down the sides to the outer edge of the velum where they connect with the circular canal (*cir. can.*). Throughout most of the length of the radial canals are lateral branches or diverticula (*div.*).

The gonads (*gon.*) are suspended in four groups, one along each of the radial canals where they leave the stomach pouch. They are long, finger-like structures, in advanced stages reaching nearly to the bottom of the bell. They vary in number from four to eleven in each group, averaging about eight.

Around the rim of the bell are found in mature forms from forty to one hundred and fifty tentacles (*tent.*) arranged in from two to four circular groups or rows. Fewkes (1889) gives only three rows. The number varies from as few as eight in the smallest forms (four radial and four inter-radial) to one hundred and sixty in the largest adults. These seem to have been added four at a time or in multiples of four, since those 2 mm. in diameter have twelve to sixteen, those 3 mm. in diameter twenty-four, and so on, only a very few having an odd number. The size also differs, usually the smaller ones being on the inner rows (see pl. 14, fig. 3). In the immature and half-grown specimens those tentacles on the four radial canals are larger than the others, but this difference becomes negligible in adult forms. These four remain, however, a trifle higher on the bell (pl. 14,

fig. 3) and thus stand out more prominently and their basal tentacular bulbs are also larger.

When the animal is resting quietly at the surface of the water and fully relaxed, the tentacles may become extended to twice the length of the bell. They are very sensitive to touch and, when slightly disturbed, and often apparently for unknown causes, the tentacles contract, either singly or all at once to much less than the length they attain when relaxed. If suddenly or forcibly disturbed the animal sharply contracts the velum, constricting the bottom of the bell till it becomes at times almost globular. The tentacles are then folded inward and contracted until only short thick stubs are seen. This is the condition often assumed in death or upon treatment with fixing agents.

The animal moves about by quick jerky contractions of the velum and bell muscles—those along the four radial canals being most apparent—so that the space within the inner bell surrounding the manubrium is suddenly diminished. The water thus forced out the opening in the velum gives a push to the bell that impels the animal forcibly in the apical direction, much after the manner of a squid when water is forced out of its siphon.

All medusae have marginal bodies situated on the rim of the bell, though their number, structure, and position are variable. These marginal bodies may be either auditory, olfactory, or visual in function. Only in very rare cases (*Staurostoma arctica*) are any two kinds of such bodies found on the same animal. It is on this basis that the Hydromedusae are divided into Ocellata, with eye-spots, and Vesiculata, with otocysts. The position of the ocelli is sometimes directly on the rim but more often at the base of the tentacles. In *Lizzia* these visual organs are found on the underside of the tentacle, which is rather unusual. This is related, however, to the fact that *Lizzia* holds the tentacle up in a vertical direction and its lower side with its eye-spot is thus turned toward the light.

In *Polyorchis* we find an eye-spot or ocellus (*oc.*, pl. 13, fig. 1, pl. 14, fig. 3) on the outer surface at the base of each tentacle where it leaves the rim of the bill. These purple eye-spots are termed ocelli, since they are regarded as one of the primitive types of eyes. At this junction the tentacle becomes thickened to

form a little cushion or bulb. Where this ridge-like thickening comes in contact with the rim (*r.*, pl. 13, fig. 1) of the bell a saucer-like depression (pl. 14, fig. 5) is formed. On the cushion and extending into the depression is located the eye-spot, which can be detected by the naked eye only as a little patch of reddish-purple pigment (*oc.*, pl. 13, fig. 1).

The pigment is not always in a round mass as one might be led to suspect. It consists of two colors, red and brown, and assumes in the living form numerous and varied shapes and manners of distribution of the colors, even in the same animal on different tentacles (pl. 15, fig. 8). Some of the masses are seen to be concentrated into a very deep, dark, red-and-brown—almost black—dot, with no outlying granules. In others the red is scattered evenly throughout the saucer-like depression with apparently no concentration at any point. Another appears with scarcely any pigment, so that only a suggestion of pink over the surface is seen. Several seem to contain a large amount of red pigment either concentrated about a large, dark-brown center with only a few scattering red grains, or running out from the brown center in various ways (pl. 15, fig. 8). There may be a single, long narrow streak running distally from the center for a distance of two or three times the diameter of the cushion. Again there may be two red lines running distally for an equal or for unequal distances, while one line may contain a considerably larger amount of pigment than the other. Or it may assume the form of a wide lobe extending down over the cushion from the brown mass. A general downward tendency is noticeable in these pigment streamers.

A single tentacle examined in section with the low-power (pl. 14, fig. 5) reveals the eye to be a cup-shaped or bud-like swelling formed by the thickening of the ectoderm of the tentacle at that point. The lower edge or rim of the cup is a little larger or higher than the upper. Viewed from the side, the center of the cup-like depression is seen to be nearly filled by a little, clear, cone-shaped projection. This extends almost to the edge of the rim and in some cases protrudes beyond it. This is the lens or "glass body" (*ls.*, pl. 14, fig. 4). The bottom of the cup is filled with dark-brown and red pigment extending out in all directions

from the base of the lens. Viewed from above, the lens body cannot be distinguished, as only a round mass of pigment is apparent.

A radial section through the lower part of the bell and tentacle (pl. 15, figs. 4 and 5) shows the general arrangement of the eye-spot with reference to the surrounding parts of the bell. The circular canal (*cir. can.*) is seen in cross-section. Extending from it is the branch canal (*tent. can.*) into the tentacle which is attached for a part of its length to the base of the bell. The main part of the bell consists, on the external side, of a thin epithelial layer of low columnar cells of the outer ectoderm (*o. ect.*). At the base of this layer, lying along the basal membrane (*bas. m.*) are longitudinal (*l. mus. fib.*, pl. 14, fig. 4) and circular (*circ. mus. fib.*) muscle fibers which extend all over the surface of the outer part of the bell, thus making a broad, muscular layer underneath the epidermis. On the inner side of the bell (pl. 14, fig. 5) is a similar epidermal layer underlaid by a circular muscular layer (*circ. mus. fib.*). Between these two external layers of epidermis lies the transparent non-cellular mesogloea (*mes.*) which forms the jelly-like contents of the live animal. Embedded in or extending through the matrix near the inner wall of the bell is what at first appears to be a thin layer of cells similar to those of the outer surface. Close inspection reveals it to be composed, not of a single, but a double layer of more or less compressed cells, the entoderm (*ent.*). The basal membrane at the base of this double row of cells extends down to the ring canal (*cir. can.*), where it turns, forming the basal membrane of the tentacle, the eye, and the outer epithelium of the exumbrella. The connective tissue at the base of the subumbrellar epithelial layer extends down around the inner part of the ring canal through the length of the velum.

At the base of the velum near the ring canal the epithelium becomes very much thickened, being more so on the lower than the upper side (pl. 14, fig. 5, *n. r., 2* and *1*) in two nerve rings. These will be discussed later.

The epithelium continues along both faces of the velum as a thin layer of cells, but the ectodermal structure of the tentacle becomes very much modified and specialized. This gradually

becomes thickened in the contracted condition (pl. 14, fig. 3) from the thin layer at the base of the tentacle to its broad, dense tip. The surface epithelium on the tentacle consists of two kinds of cells, long cylindrical cells extending to the basal membrane, and shorter pointed cells which end in a threadlike process (pl. 14, fig. 7) which may or may not extend to the basal membrane. Slender spindle-shaped cells are interspersed between those of the columnar epithelium. Nematocysts are found in irregular-shaped or round cells that seem to be crowded between the other epithelial cells, or in places supplanting the latter altogether. These nematocysts are of two kinds, a large, oval, thick-walled type, with a long tube and a large barb at its base and a smaller, more oblong type with a long tube arising from a bulb-like process and a small barb at the base. These are found largely in bunches over the surface of the tentacle and even the surface of the eye (pl. 14, fig. 6, *nem.*). Lying at an angle to the other cells or parallel to the basement membrane are large bipolar cells, each of which contains a very large, round nucleus (pl. 14, fig. 6, *n. c.*). These are probably nerve cells. Multipolar cells are also interspersed throughout the base of the ectodermal layer.

The endodermal cells which line the ring canal are of a long finger-like form, extending from the basment membrane out to the lumen of the canal. Their nuclei are somewhat ellipsoidal in form. These same columnar cells become gradually differentiated in the tentacle to very long cells, with blunt ends facing the tube, and finely drawn-out pointed ends turned towards the outside of the tentacle. These are the type found just underneath the eye (pl. 14, fig. 6). Wedged in between their basal ends are similar cells, with both ends, however, drawn out to a point. A cross-section of the tentacle through the eye is shown in plate 14, figure 7.

The general arrangement of the parts of the eye is shown in plate 14, figure 5. The epithelium of the tentacle becomes thickened to form the sides of eye cup, whose bottom is lined with a semicircular mass of brown pigment. The lens (*ls.*) body fits into the hollow of the cup. The rest of the eye-spot is formed of epithelial cells with varying functions. The whole structure of the eye seems to rest upon the basement membrane.

Under higher magnification the ocellus (pl. 14, fig. 4) reveals a great differentiation in its cellular structure. The pigment cells (*r. pig. c.*, and *br. pig. c.*) are the most conspicuous and occupy about half the entire eye. They are four to five times as long as broad, are somewhat rounded at their periphery, while the inner ends are drawn out more or less to a blunt point. They are arranged radially, from the inner surface of the depression. Those situated centrally extend from the bottom of the lens almost to the basal membrane below. All bear a nearly spherical nucleus at their inner ends just before they begin to taper. The nucleus is sometimes masked by the abundance of pigment which is found distributed throughout the cells, being denser towards their upper ends than towards their lower ones. These cells are not placed in close conjunction with each other but small spaces are left between them which are filled by the projections of the spindle or club-shaped retinal cells (*ret. c.*) which alternate with the pigment cells. These correspond to the so-called "Sehzelle" of the Hertwigs (1878). They are not all uniform in shape, those near the center being somewhat larger and less spindle-shaped. The long, narrow neck which reaches up to the base of the lens suddenly widens below the pigment cells into the broad, rounded portion of the cell, and then either rounds off abruptly or tapers to a more or less pointed end. This pointed end is more characteristic of the outer than of the deeper cells. The latter may often be bent at quite an angle to the neck portion. The nucleus is larger than that of the pigment cells and is situated at the widest part of the cell. This makes this layer of large nuclei come at a lower level than do the smaller ones of the pigment cells.

The sensory cells and pigment cells give place peripherally to the modified epithelium of the eye (*ep. c.*). Throughout the entire surface of the eye outside of the lens this type of cells is found. They vary slightly as to size and general shape, but on the whole maintain a fairly uniform structure. They are broad at their periphery, which ends in the thin cuticle above them, and then gradually taper to a long drawn-out point, always pointing away from the surface of the eye. The resemblance between the pigment cells and this peripheral sensory epithelium is so close, and the one blends so evenly into the other, that the pig-

ment cells might readily be taken for modified sensory epithelium, since a few of these peripheral epithelial cells (*ep. c.*, pl. 14, fig. 4) contain a small amount of pigment. Alternating with these are elongated spindle-shaped sense cells (*sens. c.*) corresponding to the retinal cells below the lens, with both ends drawn out to a fine thread. They are longer than the epithelial cells and extend one-fourth to one-third of the distance to the base of the eye. These are the "Sinneszelle" of Linko (1900). In the remaining parts of the ocellus is found a variety of all these structures. The basal membrane (*bas. m.*) becomes thickened in places and gives off branches (*sup. conn. tis.*) into the eye. These in turn give off smaller branches which lie in between the cells. These thin processes probably give greater strength to the eye. Lodged between them are three kinds of spindle cells: one similar to the sense cells with an oblong instead of ovoid nucleus; a second very similar, with its pointed ends drawn out to a fine thread, both possibly sensory; a third with a short, thick cell-body, short pointed ends, and a very large, conspicuous nucleus. Cells (*n. c.*) similar to the last are also found lying parallel to the basal membrane, or at an angle with it. These are not always symmetrical in form and appear to be nerve cells, or small ganglion cells. Also parallel to the base are smaller spindle cells with small nuclei and ends drawn to a finer point. These are the bipolar ganglion cells (*bip. n. c.*). Interposed between the main mass of cells is an entirely different form, the multipolar or ganglion type of nerve cells (*gang. c.*). It is triangular in outline, with a large centrally located nucleus. At each corner is a long, fine process or fibre, two of which run for some distance between the other cells, and the third extends towards the basal membrane. A similar one with only two processes is shown at the opposite side of the section.

The lens (*ls.*) fills completely the cup formed by the wall of pigment cells. When isolated it forms a biconvex lens which the Hertwigs (1878) believe effects a dispersal of light rays. They believe it to be only a thickening of the cuticle which everywhere else forms a thin transparent layer over the external surface. In some forms, as *Hippocrene* and *Sarsia*, pigment granules have been found in the lens, which led Agassiz (1849) to consider it

to be a simple continuation of the ends of the pigment cells. No pigment was found in that of *Polyorchis*. Although in some sections the lens in *Polyorchis* appeared to be the continuation of the cells of the eye, in others the line of demarcation seemed clear cut, so that no final conclusion could be drawn as to its relations. The fact that the lens easily broke loose in macerations and appeared as a biconvex body might point to its being a separate structure and perhaps a modification of the cuticle.

The peripheral nervous system of *Polyorchis* has its main location in the subumbrella and tentacles, and resembles that of the general type of medusoid forms. According to Chun (1902) and Romanes (1898) the lower forms of medusae have only a few nerve or ganglion cells scattered beneath the surface, with no indication of gathering to form continuous strands. This is especially true in the lower Anthomedusae. In the Leptomedusae, however, a higher development is found in that the bipolar nerve cells meet in their end processes, which lie adjoining each other, to form a sort of cord or nerve ring at the base of the bell. Interspersed at intervals along the cord are multipolar or ganglion cells. These may be massed in groups of from two to several to form ganglia. This is shown in *Lizzia* (see Hertwigs, 1878), in which the tentacles are grouped in four bunches of eight each. At the base of each of these sensory bulbs the nerve cord becomes much swollen and a number of ganglion cells accumulate here. The nerve ring lies entirely in the ectoderm between the layer of muscle fibers and the epithelium. It usually consists of two parts, the upper and lower, separated by branches of the connective tissue, though Linko (1900) reports in *Catablema* only a single region. This separation into two parts is only an incomplete division, as in most forms are found small fibers or strands piercing the membrane between the two parts and thus partially uniting them. Agassiz (1849) says in describing *Sarsia*: "The nervous system consists of a simple cord of a string of ovate cells, forming a ring around the lower margin of the animal, extending from one eye-speck to another, following the chymiferous tube, and also its vertical branches, round the upper portion of which they form another circle. . . . From the upper ring threadlike cells are traced downward along the proboscis." In *Sarsia* is

found also the significant thickening at its four sensory bulbs from which Linko (1900) traced branches to the eye. The Hertwigs (1878) state that the two rings probably have different functions; that the upper controls the sense organs while the other gives off nerves to the muscular parts or motor organs. They explain this difference from the fact that the motor organs lie on the under side of the protecting velum while the sense organs are on the upper side where they come in constant contact with their surroundings. In *Polyorchis* the two nerve rings (pl. 14, fig. 5, *n. r., 1* and *2*) are found. The lower nerve ring is the larger, being composed of a bunch of nerve cells with their long axes parallel to the rim of the bell. The cross-section of these cells is shown at *n. r. 2*. The upper nerve ring consists of only a few rows of cells arranged in one layer along the basal membrane (*n. r. 1*). These are much larger than those of the lower and contain very large nuclei. All the cells observed of both rings were bipolar.

Plate 15 shows isolated nerve cells, from the eye and adjoining base of the tentacle, obtained from the macerated preparations. Several types of nerve cells were thus found which were almost impossible to observe in sections. No definite arrangement of these cells was found, but a larger number was obtained from about the base of the eye than from any other part of the tentacle, which might indicate that there is an accumulation of these cells at this place. Of these the multipolar type shows the highest grade of development. The usual form is that of a somewhat triangular central portion, containing a large nucleus at or near the middle, and out-branchings at two or all three of the corners (pl. 15, fig. 14). These branches may extend for some distance with no apparent divisions, or they may divide into smaller divisions until presumably they form a fine network of interlacing fibers; though if such be the case they were broken in the preparation so that only the trunks of such branches were left. Plate 15, figure 12, shows four such cells with their processes crossing a number of muscle fibers. That these multipolar cells occupy a definite place in the eye is shown in plate 14, figure 4. The two upper branches from it ramify through the spaces between the cells, but no direct connection between the fibrillae of the ganglion

cells and the processes of the other cells of the eye was found, though such a connection may exist. Eimer (1878) mentions such a connection though he does not demonstrate its presence.

As to the connection between the nerve cells of the eye and those of the nerve ring nothing definite could be determined. Among the diversified cells of the tentacle were found (in the cross-section through the tentacle already referred to (pl. 14, figure 7) from eight to ten small spindle-shaped cells with their drawn-out ends overlapping, so that a semblance of a cord or chain of cells was found. This was found to be three cells deep. These cells have every appearance of being nerve cells, and if so, since they are found only on a plane through the center of the eye, the fact can be explained only on the basis of their being a branch of some nerve, perhaps of the nerve ring and connecting it with the sensory part of the eye.

That a nervous connection exists along the margin of the bell is shown by Romanes (1898) in his experiments on jelly-fish. He found that, with the single exception of *Sarsia*, the removal of the extreme periphery causes permanent paralysis of the locomotor system. He also found that a nervous connection unites the tentacles with one another and also with the manubrium, since all physiological connections were destroyed by radial cuts between the tentacles, while if no cuts were made the co-ordination between two adjacent tentacles was apparent.

When examined under a high power the pigmentation of the eye-spot shows many unique characteristics. The difference in distribution of the two kinds, red and brown, has already been mentioned. The structure of these two seems entirely unlike. The brown pigment consists of round, fine-grained, uniform-sized granules occupying definite positions. On the other hand the red is easily distinguishable by its coarser-grained, irregular, uneven-sized granules and its wide range of distribution. In the isolated pigment cells (pl. 15, fig. 11) this difference is clearly shown (see also pl. 14, fig. 4). The large ball-like mass of the coarser granules found among the smaller grains of both kinds is characteristic of the red pigment. This peculiar lumping together of the separate granules is never found in any but the red, though some of these red masses found in the pigment cells may be cov-

ered with a layer of the finer brown grains; this gives the appearance of a brown mass, but upon breaking open these globules the red core is always found. These balls are found scattered promiscuously throughout the eye and surrounding tentacle. Plate 15, figure 9, shows an eye-spot in which an unusual number of these masses is present. Figure 10 is one of these much enlarged. Although the finer granules of the red pigment are found in the epithelial cells of both eye and tentacle, and even to a smaller extent in the adjacent spindle cells, the largest bunches are of too great a size to be contained in any of the type cells of the eye. Some of these appear to be great accumulations of pigment granules lying in intercellular spaces, but these are probably enclosed by a distended cell wall, since several of the large ones (though not the largest) were found both in sections and macerations to have a distinct wall and nucleus (pl. 15, fig. 11). In composition as well as structure the two pigments differ. Although when stained with Delafield's haematoxylin and eosin little differentiation is seen, when phosphotungstic acid haematoxylin or Mallory's connective tissue stain is used the difference become very marked. With the phosphotungstic the brown remains the same color but the red turns to a yellowish pink. With Mallory's stain the brown still maintains its natural color, while the red assumes a greenish-blue tint with either the green or the blue predominating. When treated with acids the two pigments behave quite differently. Dilute sulphuric acid dissolves both; with nitric all the brown seems to be preserved while only the red which is mixed in with the brown is left, a thing which is also true with oxalic acid. Figure 11*b* shows an isolated epithelial cell which contains no pigment. Both forms of pigment are found in the eyes of the very small forms as well as in those small ocelli of the undeveloped tentacles of adult specimens, but the brown seems to be the dominant type.

Very little difference was found in the general structure of the of immature animals compared with the adult forms. The number of the cells was necessarily fewer and also smaller in size, but the usual arrangement of epithelial, pigment, and sensory cells was the same in both. There seems to be no definite period in the life of *Polyorchis* when tentacles, with the correlated

eye-spots, are not being added, since very small buds were found in the largest specimens measured. Tentacles only 2 mm. long were found to contain a small eye-spot.

Compared with other naked-eyed Medusae, *Polyorchis* presents many points both of similarity and contrast. All have the eye-spots located on or near the base of the tentacles and usually on the upper side, though, as mentioned above, *Lizzia* is an exception to this rule. Whenever the eyes are borne on the lower or inner side of the tentacles, the latter are carried upward at the protective rim. The eyes may be arranged around the margin, as in *Polyorchis*, or in bunches to correspond with the bunches of tentacles, as in *Hippocrene*.

In the lens type of eye the sensory epithelium, pigment cells alternating with sensory cells, and bipolar or multipolar nerve cells, are found in every case, though the form and general arrangement of cells may vary, as in the case of the sense cells of *Codonium princeps* which are long, bottle-shaped cells with a knob-like swelling near their outer ends.

Pigmentation without the lens structure is found in such forms as *Syncoryne*, *Oceania*, *Corymopsis*, *Turris*, and *Bougainvillia*. The eye-spot may be either a simple collection of pigment in the ectoderm or a more highly developed organ through the presence of a light-refracting body.

Transmitted May 3, 1913.

BIBLIOGRAPHY

Agassiz, A.

1862. "Classification of the Hydroidae" *in* "Contributions to the natural history of the United States of America" (1862), 4, 336–372.

1865. North American Acalephae. Illustrated catalogue of the Mus. Comparative Zoology at Harvard College, 2, Mem. Mus. Comp. Zool. Harvard College, 2, No. 2, pp. 118–121, 130–134, figs. 179–183, 202–214.

Agassiz, L.

1849. Contributions to the natural history of the Acalephae of North America. Pt. I. On the naked-eyed medusae of the shores of Massachusetts in their perfect state of development. Mem. Amer. Acad. Arts and Science, N. S., 4, pp. 221–312, pls. 1–8.

Allman, G. J.
1871–1872. A monograph of the gymnoblastic or tubularian hydroids (London, Ray Soc.), xxiv + 450, pls. 1–23.

Bancroft, F. W.
1904. Note on galvanotropic reactions of the medusa *Polyorchis penicillata* A. Agassiz. Univ. Calif. Publ. Physiol., 2, 43–46, 4 figs. in text.

Chun, C. und Will, L.
1902. "Das Nervensystem der Hydromedusen" *in* "Coelenterata" (1891–1902) *in* Bronn, Klass. und Ordn. des Thierreichs, 2, Abth. 2, pp. 339–362, 7 figs. in text.

Claus, C.
1883. Untersuchungen über die Organisation und Entwicklung der Medusen (Leipzig, G. Freytag), [iii] + 96, 20 pls., 3 figs. in text.

Conant, F. S.
1898. The Cubomedusae. (Baltimore, The Johns Hopkins Press), xvi + 61, 8 pls.

Eimer, T.
1878. Die Medusen: physiologisch und morphologisch auf ihr Nervensystem (Tübingen, H. Laupp'schen Buchhandlung), vii + 277, 277, 13 pls.

Eschscholtz, F.
1829. System der Acalephen (Berlin, Ferdinand Dümmler), vi + 190, 12 pls.

Fewkes, J. W.
1889. New invertebrates from the coast of California. Bull. Essex. Inst., 21, 103–107, 7 [+2] pls., [1] fig. in text.

Forbes, E.
1848. A monograph of the British naked-eyed medusae, with figures of all the species (London, Ray Soc.), viii + 104, 13 pls.

Fowler, G. H.
1900. "The Hydromedusae" *in* E. R. Lankester, "A Treatise on Zoology" (London, Adam and Charles Black), 2, chap. 4, pp. 1–59, 56 figs. in text.

Haeckel, E.
1880. Das System der Medusen; Erster Theil, eine Monographie der Medusen (Jena, Fischer), xiv + 762 + 80, 40 pls.

Hargitt, G. T.
1903. Regeneration in Hydromedusae. Arch. f. Ent.-mech., 17, 64–91, pls. 4–7.

Hertwig, O. und R.
1878. Das Nervensystem und die Sinnesorgane der Medusen (Leipzig, F. C. W. Vogel), viii + 178, 10 pls.

Huxley, T. H.
1849. On the analogy and affinities of the family of the medusae. Phil. Trans. Roy. Soc. London, 1849, pt. 1, pp. 413–434.

Linko, A.
1900. Ueber den Bau der Augen bei den Hydromedusen. Mem. Acad. Imp. Sci. St. Petersbourg (8), 10, no. 3, pp. 1–23, 2 pls.

Mayer, A. G.
1909. The medusae of the world. Vol. 1. The Hydromedusae. Carnegie Inst. Publ., **109**, 1, [iv] + 230, pls. 29.
Murbach, L., and Shearer, C.
1903. On the medusae from the coast of British Columbia and Alaska. Proc. Zool. Soc. London, **1903**, 2, 164–192, pls. 19–22.
Romanes, G. J.
1875. Preliminary observations on the locomotor system of medusae. Phil. Trans. Roy. Soc. London, **1876**, 269–324, pls. 32–33.
1898. Jelly-fish, star-fish, and sea-urchins (New York, D. Appleton & Co.), vi + 253, 63 figs. in text.

PLATE 13

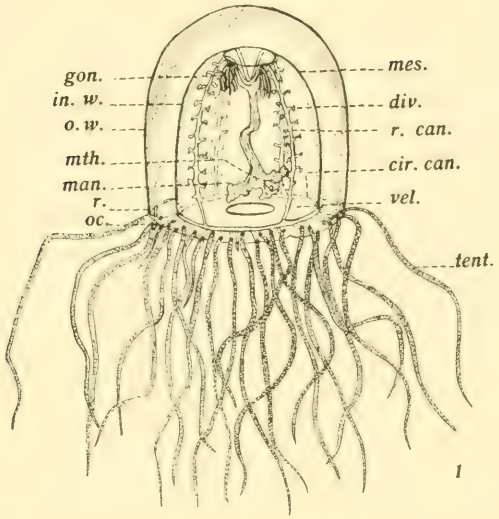
Polyorchis penicillata

Fig. 1. Lateral view of large individual at stage of sexual maturity. × 1.5.

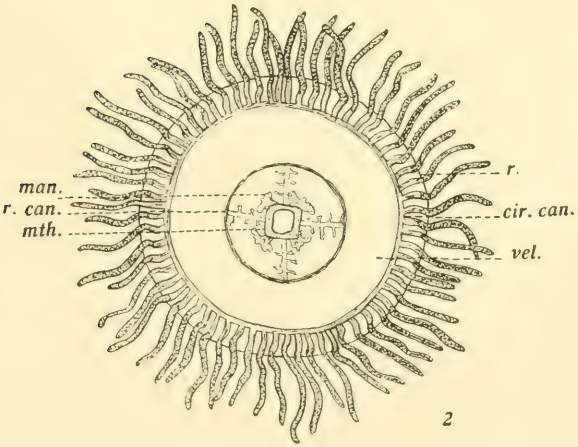
Fig. 2. Oral view of same. × 2.

ABBREVIATIONS

circ. can.—circular canal.
div.—diverticula of radial canals.
gon.—gonad.
in. w.—inner wall of bell.
man.—manubrium.
mes.—mesogloea.
mth.—mouth.
o. w.—outer wall of bell.
oc.—ocellus.
r.—rim of bell.
r. can.—radial canal.
tent.—tentacle.
vel.—velum.


gon.
in. w.
o. w.
mth.
man.
r.
oc.
mes.
div.
r. can.
cir. can.
vel.
tent.

1


man.
r. can.
mth.
r.
cir. can.
vel.

2

PLATE 14

Polyorchis penicillata

Fig. 3. Portion of rim of bell showing ocelli and tentacles of different sizes. Tentacles in a contracted state. × 66.

Fig. 4. Median section of ocellus showing the finer structure of the organ. × 666.

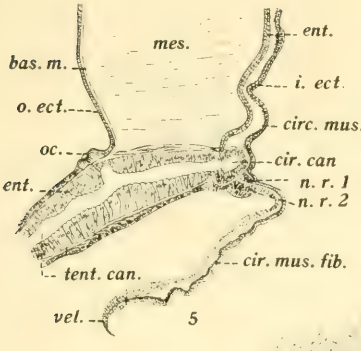
Fig. 5. Radial section through rim of bell showing relation of ocellus and tentacle. × 100.

Fig. 6. Section in radial plane through rim of the bell cutting through the margin of an ocellus. × 666.

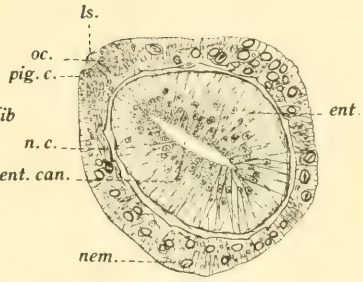
Fig. 7. Cross section of tentacle through an ocellus. × 367.

ABBREVIATIONS

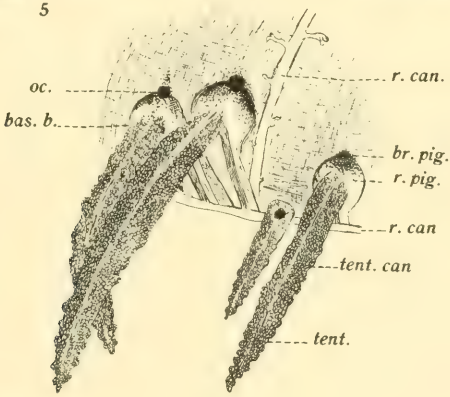
bas. b.—basal bulb of tentacle.
bas. mem.—basement membrane.
bip. n. c.—bipolar nerve cell.
br. pig.—brown pigment grains.
br. pig. c.—cell with coarse brown pigment and fine red pigment.
circ. can.—circular canal.
circ. mus. fib.—circular muscle fiber.
ent.—entoderm.
ep. c.—pigmented epithelial cell with small amount of red pigment.
gang. c.—ganglion cell with branches.
i. ect.—ectoderm lining bell.
ls.—lens.
l. mus. fib.—longitudinal muscle fiber.
mes.—mesogloea.
mus. fib.—muscle fiber.
n. c.—nerve cell
nem.—nematocyst.
n. r. 1.—inner velar nerve ring.
n. r. 2.—outer velar nerve ring.
oc.—ocellus.
o. ect.—outer ectoderm of bell.
pig. c.—pigment cell.
r. can.—ring canal.
r. pig.—red pigment grains.
pig. c.—pigment cell.
r. pig. m.—red pigment mass.
sens. c.—sense cell.
sup. conn. tis.—supporting connective tissue.
tent.—tentacle.
tent. can.—canal of tentacle.
vel.—velum.


mes.
ent.
bas. m.
i. ect.
o. ect.
circ. mus. fib
oc.
cir. can
ent.
n. r. 1
n. r. 2
cir. mus. fib.
tent. can.
vel.

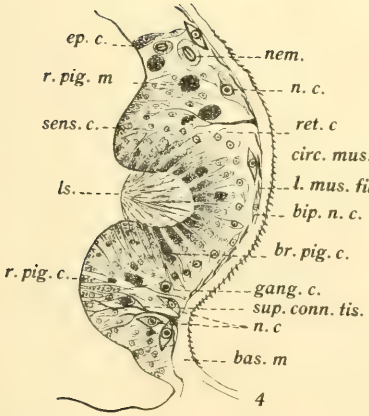
5


ls.
oc.
pig. c.
ent.
n. c.
tent. can.
nem.

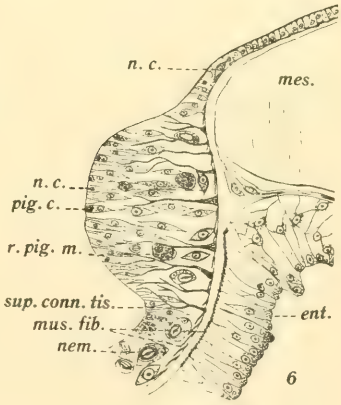
7


oc.
r. can.
bas. b.
br. pig.
r. pig.
r. can
tent. can
tent.

3


ep. c.
nem.
r. pig. m
n. c.
sens. c.
ret. c
circ. mus. fib.
ls.
l. mus. fib.
bip. n. c.
br. pig. c.
r. pig. c.
gang. c.
sup. conn. tis.
n. c
bas. m

4


n. c.
mes.
n. c.
pig. c.
r. pig. m.
sup. conn. tis.
mus. fib.
nem.
ent.

6

PLATE 15

Polyorchis penicillata

Fig. 8. Ocelli from the same medusa showing the distribution of pigment on different tentacles. The darker spot is the brown pigment at the center of the ocellus. × 14.

Fig. 9. Pigmentation of a well-developed ocellus. The darker center is the brown pigment of the ocellus. The red pigment extends peripherally from this but especially upward upon the bell and downward upon the tentacle. × 60.

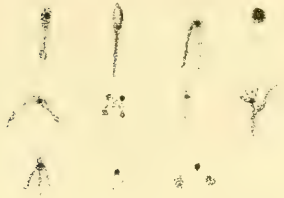
Fig. 10. A single large red pigment mass. × 666.

Fig. 11. Pigment-bearing cells of the ocellus.
a. Isolated epithelial cells with red pigment.
b. Epithelial cell without pigment. × 1300.

Fig. 12. Isolated ganglion cells from the epithelium of the tentacle near the ocellus showing interlacing of ganglionic processes with the muscle fibers. × 1300.

Fig. 13. Same showing distal branching of ganglionic processes.

Fig. 14. Isolated nerve cells from the base of the ocellus of bipolar and multipolar types.



8

11 b

11 a

10

12

9

14

13

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY
Vol. 11, No. 13, pp. 329-376, pls. 16-20 March 21, 1914

MODIFICATIONS AND ADAPTATIONS TO FUNCTION IN THE FEATHERS OF *CIRCUS HUDSONIUS*

BY
ASA C. CHANDLER

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY

Smithsonian Institution
APR 3 1914

UNIVERSITY OF CALIFORNIA PUBLICATIONS

Note.—The University of California Publications are offered in exchange for the publications of learned societies and institutions, universities and libraries. Complete lists of all the publications of the University will be sent upon request. For sample copies, lists of publications or other information, address the Manager of the University Press, Berkeley, California, U. S. A. All matter sent in exchange should be addressed to The Exchange Department, University Library, Berkeley, California, U. S. A.

OTTO HARRASSOWITZ, LEIPZIG.

Agent for the series in American Archaeology and Ethnology, Classical Philology, Education, Modern Philology, Philosophy, Psychology, History.

R. FRIEDLAENDER & SOHN, BERLIN.

Agent for the series in American Archaeology and Ethnology, Botany, Geology, Geography, Mathematics, Pathology, Physiology, Zoology, and Memoirs.

ZOOLOGY.—W. E. Ritter and C. A. Kofoid, Editors. Price per volume, $3.50; beginning with vol. 11, $5.00.

This series contains the contributions from the Department of Zoology, from the Marine Laboratory of the Scripps Institution for Biological Research, at La Jolla, California, and from the California Museum of Vertebrate Zoology in Berkeley.

Cited as Univ. Calif. Publ. Zool.

Volume 1, 1902-1905, 317 pages, with 28 plates $3.50

Volume 2 (Contributions from the Laboratory of the Marine Biological Association of San Diego), 1904-1906, xvii + 382 pages, with 19 plates $3.50

Volume 3, 1906-1907, 383 pages, with 23 plates $3.50

Volume 4, 1907-1908, 400 pages, with 24 plates $3.50

Volume 5, 1908-1910, 440 pages, with 34 plates $3.50

Volume 6, 1908-1911, 478 pages, with 48 plates $3.50

Vol. 7. (Contributions from the Museum of Vertebrate Zoology.)

1. Two New Owls from Arizona, with Description of the Juvenal Plumage of *Strix occidentalis occidentalis* (Xantus), by Harry S. Swarth. Pp. 1-8. May, 1910 ..... .10
2. Birds and Mammals of the 1909 Alexander Alaska Expedition, by Harry S. Swarth. Pp. 9-172; plates 1-6; 3 text-figures. January, 1911. 1.50
3. An Apparent Hybrid in the Genus *Dendroica*, by Walter P. Taylor. Pp. 173-177. February, 1911 ..... .05
4. The Linnet of the Hawaiian Islands: a Problem in Speciation, by Joseph Grinnell. Pp. 179-195. February, 1911 ..... .15
5. The Modesto Song Sparrow, by Joseph Grinnell. Pp. 197-199. February, 1911 ..... .05
6. Two New Species of Marmots from Northwestern America, by H. S. Swarth. Pp. 201-204. February, 1911 ..... .05
7. Mammals of the Alexander Nevada Expedition of 1909, by Walter P. Taylor. Pp. 205-307. June, 1911 ..... 1.00
8. Description of a New Spotted Towhee from the Great Basin, by J. Grinnell. Pp. 309-311. August, 1911 ..... .05
9. Description of a New Hairy Woodpecker from Southeastern Alaska, by H. S. Swarth. Pp. 313-318. October, 1911 ..... .05
10. Field Notes on Amphibians, Reptiles and Birds of Northern Humboldt County, Nevada, with a Discussion of Some of the Faunal Features of the Region, by Walter P. Taylor. Pp. 319-436, plates 7-12. February, 1912 ..... 1.00

Index, pp. 437-446.

Vol. 8.

1. The Vertical Distribution of *Eucalanus elongatus* in the San Diego Region during 1909, by Calvin O. Esterly. Pp. 1-7. May, 1911 ..... .10
2. New and Rare Fishes from Southern California, by Edwin Chapin Starks and William M. Mann. Pp. 9-19, 2 text-figures. July, 1911. .10
3. Classification and Vertical Distribution of the Chaetognatha of the San Diego Region, Including Redescriptions of Some Doubtful Species of the Group, by Ellis L. Michael. Pp. 21-186, pls. 1-8. December, 1911. 1.75
4. Dinoflagellata of the San Diego Region, IV. The Genus *Gonyaulax*, with Notes on Its Skeletal Morphology and a Discussion of Its Generic and Specific Characters, by Charles Atwood Kofoid. Pp. 187-286, plates 9-17.

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY

Vol. 11, No. 13, pp. 329-376, pls. 16-20 March 21, 1914

MODIFICATIONS AND ADAPTATIONS TO FUNCTION IN THE FEATHERS OF *CIRCUS HUDSONIUS*

BY

ASA C. CHANDLER

CONTENTS

	PAGE
Introduction	330
Pterylography	331
Moults	331
Down Feathers	332
Ordinary Down	332
Powder Down	333
Oil Gland Feathers	334
Filoplumes	334
Remiges	336
Macroscopic Structure	336
Microscopic Structure	340
Wing Coverts	344
Greater Upper Coverts	344
Greater Under Coverts	345
Middle and Lesser Upper Coverts	346
Humerals	347
Middle and Lesser Under Coverts	347
Alula	348
Rectrices	350
Contour Feathers of the Trunk	352
Upper Parts	352
Under Parts	354
Modified Feathers of the Head	357
Facial Ruff	357
Ear Coverts	358
Post- and Supraorbital Bristles	359
Eyelashes	359
Loral and Rictal Bristles	360
Conclusions	361
Literature Cited	366

Smithsonian Institution
APR 3

INTRODUCTION

As preliminary to a study of the modifications and evolution of feathers in the various orders and families of birds, it seemed desirable to ascertain the range of variation and degrees of development displayed in the plumage of a single bird. In the selection of a species to use for this purpose, it was decided to employ one which would show as great a number as possible of ordinary types of feather modification. A brief survey of the available birds to use for this study showed that of all North American birds the Marsh Hawk, *Circus hudsonius* (Linnaeus), combined the greatest number of ordinary feather types. It possesses strong and highly developed flight feathers, well-developed tail feathers, body feathers with aftershafts, rictal bristles, eyelashes, ear-coverts, facial ruff, an oil-gland tuft, powder-down patches, ordinary down, and filoplumes.

The specimen used for the greater part of the work is number 11942 of the University of California Museum of Vertebrate Zoology. It is an adult female, taken at Riverside, California, November 2, 1887.

The most superficial glance at such a bird is sufficient to show that there is a very great difference in the structure of its various kinds of feathers. The stiff, strong flight feathers are not less unlike the soft, fluffy belly feathers than are these unlike the hairlike bristles about the mouth and eyes. Indeed it may be stated that nowhere in the vertebrate phylum can a greater diversity of integumentary structures be found on a single individual than on such a bird. That such a variety of structures, varying as widely in function as in form, should be reducible to a single type of integumentary growth, similar in origin, development, and fundamental structure, is truly remarkable.

A study of the modifications which are involved in producing this variety of form, and the extent of these modifications in feathers of various parts of a single bird's body, is the object of the present paper. Most grateful acknowledgments are here extended to Professor C. A. Kofoid, of the University of California, for his kindly aid and supervision, and to Dr. Joseph Grinnell, of the Museum of Vertebrate Zoology of the University of California, for his generous co-operation in the supply of material.

PTERYLOGRAPHY

Before entering into a discussion of the structural modifications in the feathers of *Circus hudsonius*, a few words about the general pterylography of the genus will not be out of place. In common with the Accipitres in general, *Circus* is characterized by the presence of aftershafts, a permanent covering of down feathers not confined to tracts, and a circlet of feathers at the apex of the oil gland. In working out the pterylosis of various accipitrine birds, Nitzsch (1867) stated that the general pterylographic characters of *C. pygargus* (= *cyaneus?*), *C. aeruginosus*, and *C. cinerarius* (= *cinereaceus?*) essentially agree with those of *Milvus*, *Pernis*, and *Astur*, especially in the narrow form of the tracts; in the presence on the dorsal portion of the spinal tract of two divergent rows of feathers which reach the scapular fork; in the small size of the lumbar tract; and in the shortness of the inner branch of the inferior tract. *Circus* may be distinguished from the majority of the Acciptres (*Elanus*, *Elanoïdes*, *Regerhinus*, and *Gypaëtus excepted*) by the presence of lumbar powder-down patches in two symmetrical tracts on the sides of the pelvis, the posterior portion of the spinal tract running between them. Each patch tapers off anteriorly into a narrow band which reaches the shoulders. The tarsus is feathered one-third down in front, and is essentially naked behind, the head is fully feathered, the base of the gape is furnished with bristles, and the face is given a rather owl-like expression by the presence of a facial ruff.

MOULTS

An examination of about twenty-five skins in the University of California Museum of Vertebrate Zoology indicates that *Circus hudsonius* moults but once a year, this being in July. Three specimens showed new feathers in process of growth, one from San José, California, taken July 12; a second from Modoc County, California, at an altitude of 7000 feet, taken July 29; and a third from Kenai, Alaska, taken August 4. The two California specimens are in process of moulting both the definitive

and the down feathers, while in the Alaska specimen the contour feathers have all been renewed, but the down feathers are still growing in, a fact which indicates that the down feathers are moulted slightly later than the contour feathers. The filoplumes are renewed concomitantly with the definitive feathers to which they are adherent.

DOWN FEATHERS

Ordinary Down

As intimated above, the entire body of *Circus* is covered with down feathers, this being a characteristic in which the diurnal raptorial birds agree with the water birds, and differ from the ground and perching birds, which, as adults, have down only in the apteria. The down feathers of *Circus* are practically uniform on all parts of the bird, though as a rule those occurring in the midst of the contour feathers are smaller than those in the apteria. The calamus is exceedingly short, considerably less than a millimeter long, and almost entirely buried in the skin. As is usual with birds possessing aftershafts, the down feathers, as well as the contour feathers, are furnished with aftershafts, though in this case the two shafts, on opposite sides of the umbilicus, are practically equivalent to each other. The division between the two shafts at the umbilicus may best be looked upon as a split in the quill, since the pith may always be seen projecting for some distance in front of the division into shafts. As a rule, one shaft is somewhat longer and broader than the other, but this is as likely to be on one side of the feather, which projects at right angles to the body of the bird, as on the other, and it is not likely that this difference in size should be looked upon as significant of a differentiation of shaft from aftershaft. At the base the shafts of the down feathers are as broad as the diameter of the calamus, i.e., about 0.20 to 0.25 millimeters, but it decreases rapidly with each pair of barbs given off and entirely breaks up into barbs in from 3 to 7 millimeters. The barbs are exceedingly numerous, being about twelve per millimeter on each side, or over six times as many as on an ordinary flight feather or covert. The barbs are extremely long

and slender, some of them reaching a length of 25 millimeters, with a diameter of only 0.02 millimeter. The barbules, averaging about thirty-five to thirty-eight per millimeter on each side, are so fine and slender as to be scarcely visible to the naked eye. Though they may reach a length of 4 millimeters, they are scarcely over .005 millimeter in diameter. The individual cells of the barbules are from 0.06 to 0.15 millimeter long, and often bear at their distal ends two tiny prongs, which are rudimentary barbicels. The result of the density and length of these barbules is a cottony texture of the feather, and a covering for the body which could hardly be improved upon for the purpose it serves. The innumerable slender barbules are so dense as to produce a waterproof covering, and yet the air spaces between the barbules render it practically a non-conductor of heat, thus affording a very efficient heat insulation. In addition to this, it has an entirely negligible weight, giving therefore a minimum of wear and tear and waste of energy and a maximum of efficiency.

Powder-Down

The powder-down feathers in general structure closely resemble the ordinary down feathers of the body, but are at once recognizable by their peculiarly matted appearance, due to the masses of powdery substance adhering to the barbs and barbules. The proximal portion of the feather is most heavily laden with the substance, and, in addition, the barbs and barbules are always imperfectly differentiated, remaining partially fused as in a growing feather. There is no evidence of the tips of the barbs or barbules breaking down to produce the powder, as stated by Pycraft (1910), and the fact that the powder is most abundant near the base of the feather would further militate against this view. Nitzsch (1867) suggested that the powder was continually poured forth from the open end of the calamus, but this does not seem probable. The most probable explanation, it seems to me, is that a considerable portion of the feather germ, instead of developing into barbs and barbules, is stimulated by some unknown cause to break down into a fine powder, which adheres to the barbs and barbules, often in regularly shaped oval masses.

holding together several barbs or barbules. Probably just as much of this powder is produced with the part of the feather first formed as with the later part, but due to the spreading out of the feather, and the using up of the powder, it has a less dense appearance.

In powder-down feathers the barbs are attached more or less evenly entirely around the umbilicus, thus differing from the ordinary down feathers, which always have a distinct though short shaft on either side.

Oil-Gland Feathers

A further modification of the ordinary down feathers is to be found in the "tuft" of the oil gland. On close examination this tuft is found to consist of a single circlet of feathers, fourteen in number in all three of the specimens in which they were counted. The calamus of these feathers, which is about one millimeter long, is entirely imbedded in the skin. The majority of the barbs, about twenty to twenty-five, spring from the umbilicus in small groups of two to four, i.e., the calamus breaks up into a number of short roots, which almost immediately break into from two to four barbs. There is developed, however, on one side of the quill a single shaft which is very short and rudimentary, but nevertheless a constant feature. The barbs reach a length of approximately one centimeter or less, and bear a series of short, undifferentiated, awl-shaped barbules, averaging 0.54 millimeter in length, and inserted about fifteen per millimeter on each side. These barbules, differing so greatly in length from ordinary down barbules, differ further in that they lie quite closely appressed to the barbs, instead of spreading. The function of this circlet of small feathers, which is lacking in many groups of birds and is so characteristic of others, is quite unknown at the present time.

FILOPLUMES

Filoplumes, though nowhere overdeveloped or conspicuous, are found in considerable numbers at the base of the contour feathers of the dorsal, lumbar, and caudal tracts. These peculiar

feathers grow out in little bundles of from five to eight (pl. 16, fig. 2) on one side of the calamus of the contour feathers, and they lie on the dorsal side of the feather to which they belong. Invariably the filoplumes of a single bundle vary greatly in length, ranging from 2 or 3 to 40 millimeters, usually no two being of the same length. The longest ones found were attached to the posterior row of under tail coverts. They are exceedingly slender, being from 0.03 to 0.05 millimeter in diameter, and entirely unbranched and unmodified up to the last few millimeters, which may simply bear a series of barbules, or may break up into two or three barbs, each with its own barbules (pl. 16, fig. 1). The barbules, which are widely spaced, there being eight to fourteen per millimeter on each side, are entirely unmodified and comparatively rigid, although filamentous and somewhat over a millimeter long. The macroscopic appearance of these feathers is like a miniature cat-tail reed, the long shaft, slender as a spider's thread, corresponding to the stem, and the barbuled tip representing the "cat-tail" itself. What function can be served by these feathers is quite inexplicable, as they appear too weak and sparse to be of any possible use.

As observed by Pycraft (1910), filoplumes are degenerate feathers, each one, before development is complete, being surrounded by a number of barbs. In *Circus* some of these barbs appear never to spread apart and become fully differentiated as in Pycraft's figure, but they remain incompletely formed, embracing the shaft of the filoplume. Pycraft intimates that this shaft is merely a stronger persistent barb, comparable to the barbs which ultimately disappear, but it should rather be looked upon as a true shaft since barbs are never branched. It is probable that the barbs which are lost belong to the shaft, but through a defect in development never become attached to it. While developing, the tuft of five to eight filoplumes with their incomplete barbs appears like a single feather germ, but their roots are entirely independent of each other. The filoplumes do not lose their deciduous barbs until some time after the contour feather has reached its full development and ceased to grow.

REMIGES

Macroscopic Structure

The most highly specialized and most important feathers of the entire body are the remiges, or flight feathers, composed of the two groups, primaries and secondaries, the former borne on the hand, the latter on the forearm.

Circus hudsonius is a bird of strong flight, and though not known to sail or soar to the extent of some of its aquiline and buteonine relatives, it is very graceful on the wing, combining in its usual mode of progression a buoyant, easy gliding, with occasional series of long, strong wing strokes. Though not indulging in it as frequently as many of the buteonine hawks, the harriers are capable of a similar spiral sailing. It is a migratory species, undertaking flights of long duration in the spring and fall.

As might be expected of such a bird, the flight feathers are very highly developed and specialized. There are ten primaries and fourteen secondaries, which produce a long, ample, moderately pointed wing, with a comparatively shallow concavity from front to back. The wing is approximately of the same relative size as is that of *Buteo*, but is somewhat more pointed. This is due to the fact that the third and fourth primaries are considerably the longest, with the second and fifth next, equivalent to each other, while the first primary is somewhat shorter than the sixth. In the more rounded wing of *Buteo* the third, fourth, and fifth are nearly equal, while in the more pointed wing of *Falco sparverius* the second and third primaries considerably outdistance the others.

The third primary, one of the longest ones, may be described advantageously as a typical primary, the points wherein the others differ from it being dealt with subsequently. The total length of the feather is 286 millimeters, of which 47 form the calamus. The latter is not quite circular in section, measuring 3.68 millimeters in diameter in the plane of the vanes, and 4.34 millimeters in the plane at right angles to them. It tapers suddenly at the root. A short distance above the superior

umbilicus there is a decided bend in the entire feather in the direction of the inner vane, and there is an even curve toward the under surface, somewhat increased at the tip, where the vanes are also somewhat rotated on their axis to comply with the different physical forces which come into play at the tip of the wing, and to permit the free passage of the air during its up-stroke.

The points of origin of the rami of both vanes have a common beginning on the lower surface at the superior umbilicus, and proceed in an even curve toward the dorsal surface, coming to the plane of the upper surface of the shaft at about the proximal fourth of the vanes.

The shaft is quadrangular in cross-section, becoming so immediately on the under surface, but remaining rounded on the upper surface to the point where the origin of the barbs reaches the dorsal surface. At this point the shaft measures 2.8 millimeters on the under surface, 1.86 millimeters on the upper surface, and approximately 3 millimeters in depth, tapering evenly from here to the tip. The under side is grooved in the middle for almost its entire length.

As is usual with birds having highly developed flight, the vanes of some of the primaries are incised, i.e., abruptly narrowed toward the tip. On the inner vane of the feather this involves no change except the shortening of the barbs, and a slight decrease in the angle made with the shaft, but in the outer vane the character of the barbs is considerably changed beyond the point of incision. The angle made with the shaft is reduced from over 40 degrees to about 7 degrees, the intervals between origins on the shaft being thereby much increased, so that whereas about eighteen or twenty barbs per centimeter spring from the shaft on each side proximad to the incision, distad to it there are only four per centimeter. In addition to this, the ramus is increased in depth, and correspondingly in strength, to such an extent that while the dorsal surface of the barb is in the same plane with the dorsal surface of the shaft, the ventral surface, at the point of origin, is in the same plane as the ventral surface of the shaft. The barbs of the outer vane are thus rendered very stiff and elastic, and hold their place, even

if deprived of their barbules. A closer examination shows that all but the most proximal rami of both vanes, at their junction with the shaft, are continued to the ventral surface of it as more or less distinct ridges, suggesting that the stiff, broad, type of barb may be the more primitive, and that the form of the outer vane beyond the point of incision may be merely a reversion to an old type, rather than a new structure. As these barbs are serviceable without barbules, this condition might be thought of as a possible intermediate condition between a reptile's scale and a normal feather, at a time when its evolution was taking place and barbules had not yet reached a perfected state of development.

From the point of view of ontogenetic development, it is easy to think of the deep type of ramus as more primitive than the shallow one. At a time when shaft and barbs are mere ridges on the inner surface of the feather germ, the shaft ridge is probably to be considered merely as a number of barb ridges combined, as described and figured by Strong (1902, p. 160, and pl. 1, fig. 2). This being the case, the more primitive condition would be that in which the barbs and shaft are of equal depth, as in the case of the comparatively primitive feathers of cassowaries and penguins. In the latter the very broad, flattened shafts, while higher in the middle than the barbs, slope off on the sides, and there is no disparagement between depth of barb and shaft at their junction. In this case, however, the similar depth is due not to the greater depth of the barbs, but to the shallowness of the shaft. In the majority of ordinary feathers, where the shaft is enlarged and deepened, the barbs have not kept pace with this increase, and are therefore not so deep as the shaft. In the terminal portion of the primaries of *Circus* and other strong flyers, as shown above, there is a re-establishment of the equivalence in depth of barb and shaft, but whether this is to be considered as a reversion, or as a new specialization, depends upon the point of view.

The inner vane is very much broader and better developed than the outer vane, its surface constituting over eighty-five per cent of the entire surface of the feather. There are no downy barbs whatever, except a few which spring from the lips of the

superior umbilicus. The incision comes at a point slightly over half way to the tip, and reduces the width of the vane from 26 millimeters to 16 millimeters. Beyond the incision there is no tapering until the tip is approached.

The outer vane, as a resistant surface, begins about 25 millimeters beyond the superior umbilicus, since the barbs proximal to that point are downy in character, and do not adhere to each other. The vane is 10 millimeters wide at its widest point, from thence slowly tapering before the sudden narrowing at the point of incision, beyond which it is only 3 millimeters wide. Proximal to the incision the barbs are 16 to 18 millimeters long, and set at an angle of 45 degrees; distal to it they are 24 millimeters long, and set at an angle of 7 degrees, the transition taking place in about one centimeter.

All of the first five primaries are very similar to the one described above, practically the only difference being in size, and in extent of incision. The first, which is the smallest of the five, 180 millimeters in total length, is most sharply curved toward the inner vane, and has the most extensive incision, especially the outer vane, which has barbs typical of the incised portion for its entire length, except a very insignificant area of normal barbs at its base. The inner vane is incised for approximately one half its length. As the shaft is not so stout as in the third primary, the barbs of the outer vane are not so heavily built, and are set somewhat closer together, there being six to a centimeter, instead of four. The second primary is in every way intermediate between the first and third. The fourth differs from the third only in the less extent of its incisions. In this feather the wide portion of the outer vane for the first time exceeds the narrow portion, while the inner vane, though narrowed, has not so sharply demarcated a point of incision. The fifth primary has these characteristics emphasized, the outer vane being only about one-third narrow, and the inner vane beginning to taper rapidly at the point where the incision would be expected, instead of becoming abruptly narrowed.

The remaining primaries, numbering six to ten, differ from the others in their uniform width, and in the sharper angle of the bend of the shaft toward the inner vane. From the sixth to

the tenth primaries there is a gradual shortening of the feathers to 182 millimeters in the tenth, together with an emphasized curvature of the shaft, and an increasing amount of poorly developed vane at the base.

The secondaries, of which there are fourteen, show a gradual transition from the outermost to the innermost. The first one is scarcely distinguishable from the last primary, the chief differences being in the more slender shaft, and in the intensified curve toward the inner vane. The tip of the feather is more broadly rounded than is the case with any of the primaries. The first eight or nine secondaries, though very similar to each other, decrease in size to 160 millimeters in the eighth, and have increasingly slender shafts. Beyond the ninth secondary the transition from primary to covert type of feather becomes more rapid. The pronounced curve toward the inner vane is gradually lost entirely, the shaft becomes very slender and flexible and the vanes become more and more equivalent in size, until in the fourteenth they are practically equal. As is very frequent among birds, the fifth secondary is absent, although its coverts are present.

Microscopic Structure

The minute structure of the barbs and barbules, as might be expected, is at its highest development in the remiges. As an example, let us study a barb from the wide portion of the inner vane of the third primary. We find that in a superficial way the barb resembles a complete feather in its structure. The ramus is a thin lamella about 0.46 millimeter deep at the base and gradually tapering toward the tip. The proximal "vane" of barbules, if such it may be called, is 0.16 millimeter wide; the distal vane, measuring to the tips of the barbules, 0.40 millimeter. While the distal vane springs from the dorsal line of the ramus for its entire length, the proximal vane slopes down as it approaches the base of the barb, so that at its junction with the shaft it arises from a place about half way down on the ramus.

The number of barbules per unit of measure gradually decreases from the base to the tip of the barb, very rapidly

decreasing at the base, and then very slowly decreasing all the way to the tip. As is the case throughout the plumage, the distal barbules outnumber the proximals. Near the middle of a barb taken from the middle portion of the inner vane there are approximately thirty-seven distal barbules per millimeter and twenty proximals. There is very little variation in this regard in barbs taken nearer the base or the tip of the feather, though there is a slight tendency for the distal barbules to decrease in number, and for the proximals to increase as either extremity of the feather is approached. In a barb taken from near the base of the feather, for example, there are thirty-four distal barbules per millimeter, and twenty-three proximals, while in one of the barbs taken from the terminal portion of the feather there are thirty distal barbules and twenty-six proximals per millimeter.

The proximal barbules (pl. 17, fig. 3) are characterized by their comparatively stout form and long filamentous tips, the latter constituting approximately one-half the total length, which is from 0.90 to 0.95 millimeter. The dorsal recurved edge is narrow, and its teeth at the bend are poorly developed. It possesses four or five narrow ventral lobes, followed by two or three incipient ones produced by mere folding. The nuclei of the cells in the barbule show distinctly in a diagonal line running from the basal ventral corner to near the dorsal edge, where the filamentous tip has its origin. There are from eighteen to twenty cells proximal to the filamentous tip.

As explained by Strong (1902), the nuclei themselves disappear from the barbules, but their position and form may still be readily distinguished in many cases by the different refractive properties of this region. Throughout this paper, where the barbule nuclei are mentioned, it is these "ghosts" of the nuclei to which reference is made.

The distal barbules (pl. 17, fig. 3) are characterized by a short base and very long tip, with a double row of well-developed barbicels. The ventral lobes are short and stout, immediately followed by four moderate hooklets, which increase in length distally. Beginning just beyond the hooklets are two rows of forward-curving barbicels, each pair representing the drawn-

out and elongated distal angles of the cells. The nuclei in the basal portion of the barbule show quite distinctly. The total length of the distal barbules is about one millimeter, of which the base occupies but little more than one-fourth.

An excellent description of the interlocking of the barbs by means of hooklets and grooves is given by W. P. Pycraft (1893), and to this paper the reader is referred for a very thorough, interesting, and lucid account of one of the most delicate and highly perfected mechanisms to be found in nature.

Distal to the incision of the feather, the barbs differ in having a deeper ramus, 1.2 millimeters deep at the base, and more nearly equal proximal and distal vanes, the proximal barbules being longer and the distal ones shorter than in the first barb described, they having a length of one millimeter with a 0.6 millimeter base, and a length of 0.76 millimeter respectively.

On the outer vane there is a considerable modification in the form of the barbules. The proximal barbules (pl. 17, fig. 5), of which there are fifteen or sixteen per millimeter, are quite different from those of the inner vane. The base is long and slender with the usual dorsal recurved edge, and a distinct line of nuclei. At the bend the cells become very clearly demarcated, and are produced at the ventral distal angles, giving a sawlike appearance. A short distance beyond, the projections become greatly elongated and curved, and assume a form comparable with that of the longer barbicels of the distal barbules, some of the best developed ones being almost hooklet-like in form. Toward the tip a few weak barbicels are developed on the dorsal side. This peculiar type of proximal barbule does not occur throughout the outer vane, the ordinary type being found toward the base of the barbs, especially on those near the base of the feather. The transition from one type to the other is easy and rapid, the barbicels being developed in increasing numbers beyond the ventral lobes, which become slightly altered in form to produce the sawlike appearance above described. The dorsal barbicels begin as short, insignificant spines. Throughout the greater extent of the barb there are six or eight barbicels developed, but toward the tip they increase in number up to ten or twelve.

The distal barbules (pl. 17, fig. 6) are short, being about 0.6 millimeter in length, and are characterized by unusually long barbicels on the ventral side, but mere rudiments on the dorsal side. The barbules of the barbs distal to the incision do not differ materially from those proximal to it.

The minute structure of all the primaries is very similar, the tenth, for example, differing from the third only in the greater length and consequent slenderness of both kinds of barbules. The proximal barbules of the inner vane of the tenth primary are about 1.2 millimeters long with a 0.65 millimeter base, while the distal ones are 1.35 millimeters long with only a 0.23 millimeter base, which is somewhat shorter than in the second primary.

The secondaries differ from the primaries microscopically only in very minor details. The inner vane is precisely similar to that of the innermost primaries in the details of its finer structure, except in the slightly narrower rami, but the outer vane differs in a few details. The distal barbules, of which there are about twenty-six to twenty-eight per millimeter on each side, differ from those previously described in having a proportionately longer base, and a stouter tip with slightly longer and less spreading barbicels. The proximal barbules are of the same barbicelled type as in the outer vane of the primaries, the only noticeable differences being in the sharper points of the sawlike teeth on the ventral side of the bend, and the somewhat better developed dorsal barbicels on the terminal portion.

As stated before, the remiges are the most important and most highly specialized feathers of the body, and, as shown here, possess a great many adaptive modifications. The elongation of the third and fourth primaries, and the large number of secondaries, are responsible for the long, moderately pointed shape of the wing, which is so well suited for the manner of flight employed by *Circus hudsonius*. The incision of the outer primaries, their inward and downward bend, the rotation of the vanes on their axis toward the tips of the feathers, the stiff, narrow outer vanes, and broad, flexible inner vanes, and the increasing flexibility of the more proximal secondaries, are all mechanical adjustments to meet the varying physical forces

which are brought to play upon these feathers during flight. The long, narrow rami of the inner vane, set at a wide angle with the shaft, and provided with long slender barbules, are eminently fitted to produce the broad, flexible inner vane required of them, while the short, wide, inflexible rami of the outer vane, set at a narrow angle with the shaft, and possessing short, stout distal barbules with long, strong hooklets, and proximal barbules with barbicels, are equally well fitted to produce the firm resistant vane which is demanded of them.

WING COVERTS

Greater Upper Coverts

Adhering closely to the root of each primary and each secondary, is an upper and a lower greater covert. The quills of the upper coverts arise dorsally to the quills of the remiges, and slightly on the outer side, while the under coverts arise squarely beneath the quills of their respective remiges. The greater upper coverts of the primaries are characterized by the sigmoid curve of the shafts. The covert calamus lies parallel to that of the primary, but at the superior umbilicus the covert shaft swings outward, so that the feather comes to lie between its own primary and the one distal to it. This is also characteristic of the coverts of the secondaries, but on account of their very short calami, the sigmoid character of the curve is not so apparent. The greater upper coverts are further characterized by the great depth of the shaft as compared with its width. At its deepest point, the shaft of the fifth covert is about two millimeters in depth, while the width is hardly more than one millimeter. The minute structure does not differ in any way from that of the remiges, the inner vane having normal proximal barbules, and the outer with the barbicelled type on the distal halves of the barbs. There are about thirty-five distal barbules and twenty-four proximal barbules per millimeter. Going from the first to the last of the series there is a gradual reduction of the shaft in size and strength, a pronounced shortening of the calamus, and an increase in the flexibility of the vanes, consequent upon a weakening of the rami.

Greater Under Coverts

The greater under coverts are peculiar in that they lie in the same position as do the remiges, thus exposing their under surface instead of the upper, as do all the other feathers of the body. They have very short calami, their chief function being, apparently, to cover the bare calami of the remiges. Their shafts are flat, straight, and very flexible, with an inconspicuous groove running a short distance out from the umbilicus. The vanes are practically equal. The barbs, of which there are about twenty-five per centimeter on the inner vane, and twenty-three on the outer, and whose rami are only 0.12 millimeter deep at the base, are furnished with the normal type of proximal barbule, the filamentous tip being long and very slender. The distal barbules have a rather short base, with two or three weak hooklets, but an extremely long tip with a double row of weak, scattered barbicels.

There is a very considerable decrease from base to tip in the number of barbules per unit of distance. On the barbs near the base of the feather the number of barbules per millimeter decreases from about forty-five distals and thirty-three proximals at the base of the barb to thirty-one distals and twenty-four proximals near the outer limit of the differentiated portion, the average for these basal barbs being about forty distals and thirty proximals per millimeter. The downy barbules on the outer portion of the barbs are in turn more numerous than the differentiated barbules immediately preceding them, there being twenty-nine per millimeter on the proximal side, and thirty-five on the distal side. The uneven distribution of these barbules on the two sides is interesting, since there can be no functional reason for such an arrangement of undifferentiated barbules. In the differentiated types, on the other hand, the proximal barbules must be spaced to accommodate the hooklets of the distal barbules, and there is therefore a correlation between the distance apart of the proximal barbules, modified by their angle with the ramus, and the intervals between the hooklets of the distal barbules. At the tip of these under coverts, the number of barbules ranges from twenty-nine distals and twenty proximals at the base of the barbs, to twenty-six distals and seventeen

proximals at the tip. These under coverts have five or six downy barbs springing from the umbilicus, which may be interpreted as a rudimentary aftershaft.

Middle and Lesser Upper Coverts

All the upper wing coverts except the greater ones lie normally with a reversed overlap, and have well-developed downy aftershafts, which are about half as long as the feather proper in the middle coverts, and still longer in the lesser coverts. The downy barbs of these aftershafts are over three millimeters long, and are silky in appearance. There are over forty such barbules per millimeter on each side.

The main shafts of all the coverts except those of the greater series are wider than deep, the dimensions shortly above the umbilicus of a middle covert being about 0.30 by 0.54 millimeter. The vanes are perfectly similar as regards their finer structure. The barbs near the base of the feather, about forty per millimeter, are downy distally, the line of demarcation between the downy and differentiated barbules proceeding in an even curve from the umbilicus until it reaches the tips of the barbs at about one-third the length of the feather. These basal barbules show the transition from one type of barbule to another in a very instructive manner (pl. 20, fig. 21). The distal barbules are transformed by a lengthening of the tip, a shortening and narrowing of the base, and a reduction, and finally a loss, of the barbicels and hooklets. The proximal barbules change in nearly the same way, the tip elongating and the base becoming narrower and more tapering, until finally it is reduced to the narrow base of the downy barbule. The fully differentiated barbules of these feathers are not as highly developed as those previously studied. The proximal barbules, about twenty-three per millimeter, are very narrow, without a sharply defined bend, and with a very slender, threadlike tip, having no rigidity. The distal barbules, twenty-six per millimeter, have only two or three weak hooklets, and have very short and rudimentary barbicels on the side opposite the hooklets; the nuclei are quite indistinct. The lesser coverts closely resemble the middle ones in general structure, but become progressively smaller in suc-

ceeding rows. The aftershaft is poorly developed, its shaft being very short, and the barbs springing more or less fanlike from a broad base. The lesser coverts on the radial edge of the wing are strongly curved in order to fit firmly, and give the smooth, sharp line for cutting the wind. The upper and lower coverts of this region curve in opposite directions, both of them away from the margin, those directly on the edge being quite narrow, and but slightly curved.

Humerals

The continuation of the lesser coverts on the humerus gives rise to a series of four or five large feathers which lie normally in an antero-posterior series, on account of the usual position of the humerus. These feathers, known as tertiaries or humerals, are remex-like in form, and devoid of aftershafts. Their minute structure is very much the same as that of the remiges, but they differ in the fact that the more distal barbs of both vanes have, toward their tips, proximal barbules with more or less hooklet-like spines, quite similar to those of the distal part of the outer vane of the remiges.

Middle and Lesser Under Coverts

The under wing coverts, with the exception of the greater coverts, which have already been described, lie as do the upper coverts, with their upper side exposed and the umbilicus toward the body of the bird. A small, downy aftershaft is present. The barbs of the basal third of the feathers are downy in nature at their tips, the most basal ones being entirely downy. There are twenty-three barbs per centimeter on each side of the inner vane, and twenty-one on the outer. The distal and proximal barbules average only twenty-one and fifteen per millimeter respectively, and, as the hooklets and grooves are very weakly developed, there is a tendency for the barbs to break apart except in the region near the shaft. The distal barbules have two or three very weak hooklets, followed by a single series of weak barbicels on a long slender tip. The proximal barbules taper to a slender tip which bears a series of small barbicels.

While in general the coverts are not so highly developed and specialized as are the remiges, nevertheless they are thoroughly adapted for their function, and show numerous adaptive adjustments which command admiration. The sigmoid curve of the quills of the greater upper coverts to bring them to lie between two remiges, the increased depth of the shaft to make them more resistant to vertical stresses, and the increasing weakness and flexibility of the shafts and vanes proximally to parallel the same condition in the remiges, are niceties of adjustment which should not be overloked. The greater under coverts are especially fitted for their function of covering the bare calami of the remiges by their very short calami and smooth flat form. Their reversed position, i.e., with the umbilicus exposed, is not an adaptive, but an ancestral character. The reversed overlap of all the upper coverts except the greater ones is difficult of explanation, unless it is possible that the wind, coming forcibly from the distal side of the feathers during flight, might be more likely to ruffle the feathers if they had the same overlap as the remiges. In these feathers, which are not subjected to the severe strains and stresses imposed upon the remiges, the minute structure is much simpler, the downy portion of the feather is increased, and the shafts are weaker. Nature is lavish only when there is need for it. The humerals, which perform an important function in bridging over the gap between the innermost secondaries and the body of the bird, are again highly developed and specialized, being almost precisely the same in form as the innermost secondaries which they follow.

ALULA

The only other feathers of the wing which merit special description are the thumb feathers or alula, consisting of four feathers at the base of the outermost primaries. Their form is a good example of structural adaptation. Obviously, to have the edge of the wing which cuts the air formed by the edges of more than one feather would result in much ruffling and loss of energy. This difficulty is avoided on the distal half of the wing by the

use of a single strengthened feather as a cutting edge, and on the shoulder region by the use of numerous very small curved feathers, making a smooth, rounded edge. In the region of the alula the same result is obtained in a different way, namely, by a very sharp curve in the outer vane of the outer thumb feather so that this fits over the edge of the wing like the ridge boards on a roof.

The four alula feathers lie one above the other, rather than in a horizontal series, so that the outer vanes of all four come to lie on the edge of the wing, and are curved as is that of the first one. These feathers are further distinguished by the groove on the under surface of the shaft swinging outwards, so that its position is nearer the outer vane.

The minute structure of the outer vane is somewhat different from that of the other feathers thus far considered. The barbs, of which there are eighteen per centimeter on each side, bear very short distal barbules (pl. 18, fig. 8), which are from 0.5 to 0.6 millimeter in total length. The tips are stout, with very long hooklets and with barbicels on one side only, thus presenting an appearance very similar to that of the distal barbules of the outer vane of the remiges, but with the short, stout form and length of the barbicels exaggerated. The proximal barbules (pl. 18, fig. 7), twenty per millimeter, are nearer to the type with barbicels hitherto described than to the normal type, but are nevertheless somewhat different. The upper recurved edge is provided with a series of short, blunt teeth, while the lower edge, for the middle third, is furnished with lobes or barbicels of various grades of development. There is no distinct bend, the base gradually tapering to the tip. The inner vane has no structural peculiarities; it has twenty-two barbs per centimeter.

The peculiar modification of the outer vanes of the alula feathers to serve a unique function, namely, that of forming a smooth, rounded edge for the wing in this region, is a very interesting adaptation. As has been shown, not only is the macroscopic form of the feather changed by modifications of the barbs and shaft, but there is also a very high specialization of the microscopic structure to produce the strong resistant vane required to adequately serve its peculiar function.

RECTRICES

Next to the remiges, the most highly developed feathers of the body are those of the tail, which are of prime importance in steering and balancing. They are commonly known as rectrices. *Circus hudsonius* possesses twelve of these feathers, growing in an arc from the posterior portion of the pygostyle, on the dorsal side. Their bases are covered dorsally by the upper tail coverts, and ventrally by the under tail coverts.

The general structure of the shaft and vanes is very similar to that of the primaries, except that the shaft is more nearly straight, and not so wide and deep. The two middle tail feathers have straight quills bearing two subequal vanes. The barbs are set at an angle of about 40 degrees with the shaft, and are 35 to 40 millimeters long and 0.6 millimeter deep at the base. Proximally there are twenty-six per centimeter on each side, gradually decreasing to fourteen per centimeter at the tip. The minute structure of the middle rectrices is peculiar in that the proximal barbules of both vanes have barbicels on the distal portion of the barbs. The distal barbules of both vanes resemble those on the inner vane of the remiges.

In the lateral rectrices there are a number of modifications. The inner vane, which in the middle two feathers is 20 millimeters wide, in all the other tail feathers is about 25 millimeters wide, while the outer vane steadily decreases laterally from 20 millimeters in the middle feathers, to 10 millimeters in the outermost one. As stated above, the tail feathers are arranged in the form of an arc, so that the outer ones are inserted at a wider and wider angle to the longitudinal axis of the bird's body. Unless some provision were made against it, this would result in the tail being in a permanently spread condition. This difficulty is overcome by an increasingly pronounced bend in the quill near its base, so that the outside feathers, though inserted at a wide angle to the long axis of the body, come to lie parallel with the more central ones. The barbs of the inner vanes of the feathers, which decrease in number from twenty-eight to thirteen per centimeter from base to tip, possess proximal barbules of the normal type only, none of them having distinct barbicels; they

are spaced about twenty per millimeter. The distal barbules, about thirty per millimeter, have short bases and extremely long, slender tips, bearing a double series of well-developed spreading barbicels. There are usually four moderate hooklets of equal size, and two strongly delimited ventral lobes. The nuclei of both sets of barbules show very distinctly.

The outer vane of the tail feathers differs decidedly from the inner vane in its microscopic structure, and the proximal barbules, twenty-three per millimeter, are of a rather peculiar type (pl. 18, fig. 9). The total length is about 0.9 millimeter, the base being long, moderately stout, and tapering to the short tip, there being no well-marked bend. The middle third of the barbule is characterized by a series of moderately stout, blunt projections, which are intermediate in form between barbicels and ventral lobes, but seem more closely akin to the latter. The nuclei of the barbules are large and conspicuous, this probably being an indication of strong growth and abundant nutrition.

The distal barbules, twenty-nine per millimeter, have a tip considerably less than twice as long as the base, bearing long brushlike barbicels on one side, and short, stout ones, or, in the more basal ones, only rudiments, on the other—a very striking difference from the long, slender barbules of the inner vane. Their total length is scarcely 0.6 millimeters.

Since the rectrices are such important feathers, and have such a necessary and difficult function, they are, as we should expect, strong, durable, and highly specialized to serve their purpose in the economy of flight. While the shaft is strong and stiff, it is not as heavily built as is the shaft of a primary, since the stresses and strains acting upon the tail in steering or balancing are not nearly so severe as those which the primaries undergo during flight. Since in the tail a broad, resistant surface is required, there is no incision of the feathers or rotation of the vanes as in the primaries, and the tips of the feathers are broadly rounded. The bend in the shafts of all the lateral feathers to bring them to lie parallel with the middle ones, and to prevent the tail from being permanently spread, is the most interesting adaptation.

CONTOUR FEATHERS OF TRUNK

Upper Parts

The ordinary contour feathers covering the trunk of the bird, which are useful for warmth and protection and for presenting a smooth and more or less elastic surface to the air, are much less developed than the wing and tail feathers hitherto described. In these feathers the downy aftershaft reaches its maximum of development, covering, as it does, over half of the under side of the feather. Though there is quite a wide variation between extreme types of these non-specialized feathers, as for instance between the crown, back, and shank feathers, there is every gradation between them, and it will suffice to describe one typical example, and then discuss the modifications on different parts of the trunk.

Taking a feather from the middle of the back as an example, we find that it may be at once distinguished from any of the feathers so far considered, with the exception of some of the smaller upper coverts, by the large proportion of the downy basal portion, and by the loose way in which the differentiated barbs are held together.

The calamus is very short for the size of the feather, being approximately 3.5 millimeters long. The shaft is comparatively slender, measuring, on the under side, about 0.47 millimeter in width at the umbilicus, but rapidly decreasing to about 0.3 millimeter, after which it decreases slowly. As in the case of the primaries, the upper side of the shaft is narrow, measuring about 0.3 millimeter at the umbilicus, and quickly decreasing to 0.2 millimeter or less. The under side of the shaft is grooved for a few millimeters above the umbilicus. The total length of the shaft in a feather from the middle of the back is about 55 millimeters.

The vanes are practically equal in size, but the barbs of the outer vanes are inserted at a slightly more acute angle with the shaft, being, therefore, of greater length and fewer in number on the inner vane.

The terminal portions of the more basal barbs are downy, some of the filamentous barbules, of which there are from twenty-

five to thirty per millimeter on each side, reaching a length of 3.5 millimeters. The line of demarcation between the differentiated barbules and the downy ones runs out farther and farther from the shaft, the distal half of the feather having no downy barbules. The distal barbules of the differentiated portion of the feather are in general very slender and weak, varying in length from 0.95 millimeter on the basal fifth of the feather, to 1.25 at the middle, and decreasing again to about 0.85 near the tip. A typical distal barbule from near the middle of the feather (pl. 18, fig. 10) has a base about 0.35 millimeter long, followed by a single lobe, and then from two to four small, weak hooklets. The long, slender tip is armed with a single series of fairly long, curved barbicels on the ventral side of the barbule, those of the dorsal side being rudimentary or absent. The proximal barbules (pl. 18, fig. 11) are of almost exactly the same length as the distal barbules opposite them, but the base is much longer, being over 0.6 millimeters, though only about 0.04 millimeters in width. At the bend, which is sharply defined only in the more basal barbules, there are three or four sharp spines, the barbule meanwhile tapering to a threadlike tip. Toward the tip of the barb, the bases of the proximal barbules taper gradually into the tips, which are filamentous and bear a double series of weak, rudimentary barbicels.

The feathers of the upper back, as compared with those of the middle back, have more barbs per centimeter on the shaft, there being twenty-two and twenty-six on the inner and outer vanes respectively, and the downy portion is considerably increased. The feathers are inserted at nearly 90 degrees to the body of the bird, and stand closer together, the shaft being, therefore, very sharply curved in order to bring the interlocking terminal portion of the feather to lie flat on the bird. The barbules are less numerous, there being eleven proximals and sixteen distals per millimeter.

The feathers of the nape are in general more elongate and narrow. They have an average of twenty-four and twenty-eight barbs per centimeter on the outer and inner vanes respectively, and have the same wide spacing of the barbules exhibited by the upper back feathers.

The feathers of the crown are shorter and more compact than the nape feathers, the down portion is greatly reduced, the barbs are about the same in number as on the nape feathers, and the barbules (pl. 19, figs. 16 and 17) are equally numerous, there being twenty-two proximals and twenty-seven distals per millimeter. From the lower back to the crown there is a gradual shortening of the barbules, as might be expected from the closer approximation of the barbs. The average length of the barbules of a crown feather is 0.5 millimeters or less for the distals, and about 0.75 for the proximals.

The most caudal row of back feathers, modified to serve as upper tail coverts, may be distinguished from the other back feathers by the much stouter shafts, and the firmness of the vanes. The shaft is over a millimeter broad at the umbilicus, and is conspicuously arched in order to fit down firmly against the quills of the tail feathers. The compactness of the vanes is due to the firm interlocking of the barbules, and to the fairly numerous barbs, there being twenty-one and thirty-one per centimeter on the outer and inner vanes respectively. The distal barbules, twenty-eight per millimeter, are very well developed, having broad bases and well-formed hooklets, followed by a single series of even, medium-sized barbicels. The proximal barbules, twenty-one per millimeter, are of typical form, with a broad base, and a well-marked bend before the stout tip. The aftershaft in these feathers is insignificant.

Under Parts

The feathers of the under parts differ from those of the back only in minor details. The feathers from the lower breast to the facial ruff are very similar to the corresponding feathers of the back except that there are two or three fewer barbules per millimeter, the result being a somewhat looser and more fluffy feather. The lower breast feathers have the downy portion very highly developed, and the downy barbules, some of them four millimeters in length, are crowded together on the shaft, thirty or more per millimeter.

The upper breast feathers differ from the lower ones but slightly. They are shorter and much more curved, the shaft

traversing an arc of 90 degrees. The quill is inserted almost perpendicularly to the body of the bird as in the upper back feathers, so that the developed terminal portion of the feather comes to lie flat on the contour of the body.

The loosest and fluffiest of all the contour feathers of the body are those of the flanks, lower belly, and legs. These feathers are considerably elongated, frequently reaching a length of eleven or twelve centimeters, and from half to two-thirds of this is entirely downy in character. The aftershaft, which is about half as long as the feather proper, and the basal third of the latter are made up of barbs with long and numerous downy barbules, the result being a dense, cottony structure. For some distance proximad to the beginning of the differentiated barbules, the feather has a very open and fragile appearance, due to the fact that the barbs are widely separated on the shaft, there being only eight or nine per centimeter, and the barbules, while still filamentous and undifferentiated, are much shorter and less numerous, those on the middle of the barb shortly proximad to the loosely interlocking portion of the feather being from 0.8 to 1.8 millimeter long, and spaced about eleven or twelve per millimeter on the barb. The barbs, which are loosely interlocking, are not provided with specialized barbules all the way to their tips, the more proximal of these barbs being held together by only a few barbules at their bases. Near the tip of the feather the barbs are not provided on their distal portion with typical downy barbules nor with normal specialized ones. Those of the distal series are very slender and tapering but not filamentous, and are practically without modification except for two or three weak hooklets about half way to the end (pl. 19, fig. 13). The proximal barbules (pl. 19, fig. 12) are slender and taper all the way to the end.

The more typical distal barbules of the breast feathers have a narrow base about 0.23 millimeter long, followed by an extremely long, slender tip, possessing usually three hooklets and a single series of weak barbicels. The total length of the distal barbules is about 1.25 millimeter, except near the base of the barb, where they are shorter. The proximal barbules are not highly specialized, having a very slender base and a threadlike

tip, each forming approximately half the length, which is 1.45 millimeters.

The under tail coverts, consisting of three or four rows of feathers back of the anus, are, in general appearance, very much like the feathers of the belly and flank, but are always better developed, possess filoplumes, and differ in some details of structure. The aftershaft is small, especially in the terminal row, but the main shaft is comparatively heavy and stiff, nearly round in cross-section, and with practically no groove on the under surface. There is no noticeable difference in form or structure in the feathers of the different rows, but they increase considerably in size from the anterior to the posterior row, those of the former being about seven centimeters long, while the posterior ones are twelve centimeters. Over half of the feather is furnished with typical downy barbs, only the distal three-eighths being provided with hooklets and grooves, these, however, being held together much more firmly than the belly feathers.

On the more proximal portion of the feather there are as many as thirty barbs per centimeter, and the filamentous barbules, two to three millimeters long, are very dense, there being about thirty-seven per millimeter on each side, thus producing a cottony apearance, but the downy portion near the middle of the feather, as in the case of the flank feathers, has a more open and fragile appearance, due to a decrease in number of both barbs and barbules. In the interlocking area, where there are twelve or fourteen barbs per centimeter, the differentiated barbules are of a higher type than those of the belly feathers. The distal barbules, of which there are about eighteen per millimeter, have bases 0.3 millimeter long, three well-formed hooklets, and a series of large curving ventral barbicels, the dorsal ones being small and weak. The total length of the distal barbules is about 0.95 millimeter. The proximal barbules, which are from 0.95 to 1.00 millimeter long, have comparatively slender, tapering bases, with a few weak, spinous ventral lobes, and a filamentous tip which sometimes bears a few rudimentary barbicels. There are about 14 of these barbules per millimeter.

It is very noticeable that the ordinary contour feathers of the trunk, which have no special function other than conservation of

heat and protection, and to produce a smooth automatically adjustable surface to the air, do not need, and do not have, the high development and numerous adaptive modifications and adjustments of the more specialized wing and tail feathers. The general loose structure and weak form of the barbules is characteristic throughout. Going from the middle or lower back to the nape and crown, there is a gradual increase in number of barbs per unit of measure, accompanied by a correlative decrease in length of barbules, the result being increasingly compact feathers. A similar tendency is shown in the feathers of the under parts. The belly and flank feathers are very long and fluffy, lying flat on the body. The lower breast feathers are shorter and more compact, and are inserted more nearly perpendicularly to the body contour; and the upper breast feathers have these tendencies emphasized, they being short, compact, and inserted directly perpendicular to the body contour, the shaft traversing an arc of 90 degrees to bring the well-developed terminal portion to lie flat. This thick, loose covering produces a high degree of elasticity and ability to smooth over irregularities of contour, resulting in a smooth surface with a minimum of unnecessary friction. The contour feathers of the under side of the pygostyle are specialized to serve as under tail coverts, while the terminal row of back feathers is considerably modified to serve as upper tail coverts.

MODIFIED FEATHERS OF THE HEAD

Facial Ruff

Some of the most interesting modifications of feathers to be found in this bird are those of the head, surrounding the eyes, ears and mouth.

Running around the head ventrally, beginning on either side just above and back of the ear, and encircling the throat, is a peculiar facial ruff, composed of specially modified feathers. The latter are very numerous and closely inserted, and project almost perpendicularly from the body of the bird. They then turn at right angles, so that the broader terminal portion lies flat on the surface. The feathers are elongate and narrow, the total length being from 16 to 18 millimeters, 10 millimeters of

which is at right angles to the body of the bird; the greatest width, which is at the turn, is about 5 millimeters. The aftershaft is, as usual, downy, and very minute. The barbs are very numerous on the shaft, there being thirty-six to forty-one per centimeter on each side, about twice as many as in an ordinary breast feather. The barbules, which, due to the closeness of the adjoining barbs, are very short, are also very closely set, there being forty-three distals and twenty-nine proximals per millimeter. The proximal barbules (pl. 19, fig. 14) are 0.62 millimeter long, while the distals (pl. 19, fig. 15) are about 0.55 millimeter. As there is no downy portion on the main shaft, the result of the structure described is a very stiff, compact feather, quite different from the loosely netted feathers to be found immediately in front of or behind the ruff. Ruff feathers from beneath the throat differ in having longer aftershafts and in being larger and less densely inserted; they are not quite so compactly woven as those of the sides of the head. The function of the facial ruff is unknown, unless it be merely in the nature of an ornament, which is unlikely, since mere aesthetic ornamention is strikingly lacking among the birds of prey. The facial ruff is present in both sexes.

Ear Coverts

Just in front of the facial ruff, extending from the corner of the gape to the upper end of the facial ruff, is a group of several dozen feathers known as ear coverts, which are wonderfully adapted to fulfill the functions for which they are designed. Obviously it would interfere with hearing to have the ears covered by normal, densely woven feathers, and, on the other hand, it would be disadvantageous to have the large open ear entirely exposed and unprotected. The ear coverts are perfectly adapted to suit these conditions in that they are extremely loose in weave, but form a network which, while it gives practically no obstruction to sound waves, effectually protects the ear from the entrance of even small particles of dust. The shaft bears about twenty barbs per centimeter on each side, which, due to the appression of their barbules, are entirely out of contact with each other. The barbules (pl. 19, fig. 18) are short and undiffer-

entiated and are closely appressed to the barbs, the only ones which stand out from each other being those which are attached directly to the shaft and fill in the angle between the shaft and the barbs. The only function of these barbules is to give an uneven surface to the barbs, in order more effectually to catch and hold particles of dust coming in contact with them. The aftershaft is over half as long as the main shaft, and has a structure almost identical with it, the barbs being, possibly, farther apart than on the main shaft.

Post- and Supra-orbital Bristles

Just back of the eye, in a line where the feathers of the crown curve down, but do not quite meet the upcurving ear-coverts, there are a few very small feathers, having a structure similar to that of the ear coverts, except that the shaft is elongated as a bristle for several millimeters beyond the tip of the barbs. Such feathers are described in the water rail by Bonhote (1911–12). The barbs are a little more numerous than they are in the ear coverts. The supraorbital feathers, between the crown feathers and the eye, are very much like the last-named feathers, the main shaft being continued naked and black for about four millimeters (pl. 20, fig. 19). The barbs appear coarse and cylindrical, due to the close appression of the filiform barbules. The aftershaft has only about half as many barbs as the main shaft and is not continued as a bristle. These feathers are very numerous in the narrow, supraorbital region of the head.

Eyelashes

The eyelashes (pl. 20, fig. 20), of which there is a single row completely encircling the eye, are among the most highly specialized, and at the same time the simplest feathers of the body. The calamus is comparatively heavy and barrel-shaped, about one millimeter long. From the hollow calamus the main shaft continues stiff, straight, and unbranched, 5.5 millimeters long, cylindrical in form, and very deeply pigmented with black.

From the umbilicus, in the position of the aftershaft, and undoubtedly representing it, are ten or twelve short, spreading barbs, with numerous appressed awl-shaped barbules. The barbs are about 0.6 millimeter in length, and the barbules 0.2 millimeter. It is interesting to note that in many birds which are devoid of aftershafts the eyelashes are entirely without barbs.

Pycraft (1910) remarks that the eyelashes of many birds, e.g., ostriches and hornbills, are akin to filoplumes. Certainly in the case of hawks the eyelashes have no relation whatever to filoplumes, as they are very evidently modified contour feathers. The steps in their reduction from ordinary contour feathers may be seen in the ear coverts and postorbital bristles, in which they show very plainly the method of their evolution. The ear coverts could never be mistaken for anything but modified contour feathers; the postorbitals differ from these only in the further reduction of barbs and barbules, leaving the terminal portion of the shaft as a stiff black bristle; and the eyelashes differ from the postorbitals only in the complete loss of the few remaining barbs attached to the shaft.

Loral and Rictal Bristles

Filling in the space between the eye and the beak are some very numerous and closely inserted feathers known as loral bristles. They are of the same type as the eyelashes, the only difference being in the sharp upward curvature, resulting in the tips of the bristles almost meeting over the beak, and partly covering the nostrils. The loral bristles are radially arranged around a point a short distance in front of the eye, so that the front upper ones are considerably longer than the others, some of the bristles being nearly fifteen millimeters long.

Filling in the space between the two rami of the lower mandible in a manner similar to that of the bristles in the loral region are the rictal bristles, which are numerous and closely inserted. They are of two types, those immediately behind the symphysis of the jaw being of the eyelash type, i.e., with a naked shaft, and a few barbs representing the aftershaft, while the

majority are of the postorbital type, i.e., a loosely woven, barbed feather with a prolonged naked shaft. All gradations between these two types are present.

Such specially modified bristles as these of the loral and mental regions are better adapted to cover these regions than ordinary contour feathers, since the latter would be more readily ruffled, worn, and soiled. Possibly the bristles are furnished with sensitive nerves at the base, as are the whiskers of a cat, and function as "feelers."

CONCLUSIONS

In the above survey of the plumage of a single species of bird, the most striking thing to come to our attention is the remarkable adaptation of the form of the several types of feathers to function, without involving much change in fundamental structure. As stated at the beginning of this paper, in such a bird as *Circus hudsonius* there is displayed a greater variety of integumentary structures, all reducible to a single fundamental type, than can be found anywhere else in the vertebrate phylum, and an attempt has been made in the foregoing pages to show exactly what modifications of the fundamental feather structure have produced the various results to be observed in diverse kinds of feathers to be found on the bird. I can think of no other mechanism produced in nature which is so complex and yet has all its parts so finely adjusted and so perfectly adapted for the function it has to serve as that of a feather. In order to obtain some idea of the complexity of a well-developed feather, a computation was made of the number of barbules present in one of the middle tail feathers of the species under consideration. The figures showed that, at a very conservative estimate, there are about 1,250,000 barbules present. If laid out end to end in a straight line these microscopic structures, appearing to the naked eye like a particle of dust, would stretch over a distance of more than 1000 meters. When the number of cells in each barbule, which is at least twenty, and the number of feathers in

a bird's body are taken into consideration, and it is realized that all the feathers are renewed at least once a year, we may get some idea of the astounding productivity of the epidermis of a bird.

Briefly reviewing the ultimate feathers produced by the different kinds of structure described, we find that while in the majority of cases it is easy to understand their function, and we marvel at their wonderful adaptation for serving it, there are a few cases where no adequate explanation for their presence has been found. Most noticeable of the feathers in this category are the filoplumes, especially when we consider their persistance, not only throughout most of the plumage of this species, but throughout the entire order of birds. The circlet of especially modified feathers surrounding the apex of the oil gland is equally mysterious so far as its function is concerned.

The perfect adaptation of the under covering of down feathers to serve as a heat-insulation has already been mentioned. The especially modified "powder-down" feathers are still an enigma so far as their use in avian economy is concerned. Various theories have been offered, but none of them seem reasonably convincing.

In the remiges we find the highest degree of efficiency attained, and not the slightest detail of the mechanism of these most important feathers has been omitted in their specialization. Not only has the minute structure attained its highest development and the maximum of perfection, in order to produce a strong, resistant feather surface, but every detail of their macroscopic structure and interrelations has been unerringly attended to, so that they are thoroughly adapted to meet the physical forces brought to play upon them during flight, and to perform their work with the least amount of friction and wear. The third and fourth primaries are elongated to produce a pointed wing, suitable for the kind of flight indulged in by the species; the shaft, and with it the feather as a whole, is bent inward and downward to produce a shallow concavity on the under surface of the wing, which, of course, serves the same purpose as the "spoon" of an oar; near the tip of the feather the vanes are somewhat rotated on their axes so that during

the upstroke of the wing they allow a free passage of air between them, but during the downstroke the force of the wind closes them together and an even, resistant surface is gained; the outer vanes are very strong and firm, but narrow and inflexible, while the inner vanes are very broad and flexible, so that the impact of the air during a downstroke of the wing is sufficient to force the wide, under-lapping part of the inner vanes up against the stiff outer vanes which act as braces, and the even resistant surface already mentioned is produced; the terminal portions of the first five primaries are abruptly narrowed so that when the wing is spread the tips of these feathers are spread out finger-like, and allow an even escape of air from under the wing; and, finally, the increasing weakness and flexibility of the innermost secondaries serves a function in the automatic adjustment of the antero-posterior concavity of the wing for swift or slow flight (see Headley, 1912).

In the remiges and rectrices there is a minimum of downy basal structure, this portion of the feather being reduced to a very few downy barbs in the region of the superior umbilicus and the lower portion of the outer vane. From the distribution of downy structure in the contour feathers in general, it would seem that inadequate nutrition was the primary cause for its growth rather than a slower rate of growth as suggested by Riddle (1908). Undoubtedly the portion of the feather germ farthest from the shaft receives the poorest nutrition, and it is significant that in all the barbs the terminal portions which lie farthest from the shaft in the feather germ have a tendency to become downy in nature. When the feather is near completion, and the nutritive supply is reduced and finally cut off, two changes take place which it seems to me must be correlated with the reduction of nutrition; namely, the change from a differentiated to a downy type of barbule, and a diminution of the rate of growth, the latter entailing a more frequent repetition of parts, i.e., a production of a greater number of barbs and barbules per unit of distance. This reduction in rate of growth was taken by Riddle to be the primary cause of the change in type of structure, but it seems more reasonable to look upon both as results, independent of each other, of the

insufficient nutrition. That the change in type of structure is due to the latter and not to the change in rate of growth is further indicated by the invariable way in which the downy structure begins to be developed at the point farthest from the source of nutrition, i.e., at the tips of the barbs, and gradually approaches the shaft. Were the change due to a change in rate of growth, all the barbs would be affected at the same level and the line of demarcation between the downy and differentiated portion would be parallel to a horizontal fault bar, i.e., almost at right angles to the shaft.

In the greater upper coverts again we are struck by the nicety of the details of structure exhibited. In this case the most noticeable special adjustments are (1) the sigmoid curve of the shaft, instrumental in bringing the feathers to lie between and not squarely above the remiges, and (2) the depth of the shaft as compared with the width, rendering it more resistant to vertical stresses, and therefore firmer. The greater under coverts are peculiar, as noted previously, in the fact that they lie with their reverse side exposed, thus differing from all the other feathers of the body. The explanation for this state of affairs offered by Wray (1887) is very suggestive, namely, that this series of coverts represents a series of feathers which at some stage in the phylogeny was equal to or larger than the next row, or true remiges, and when the latter outdistanced them and covered them up, they remained in the same relative position, but functioned as coverts. They, as well as the upper coverts, have the same overlap as the remiges, while all the other coverts have a reversed overlap. The absence of the aftershaft is an almost necessary corollary of the reversed position of the feather. In these under coverts there is a tendency for the barbules to become weaker and less specialized in structure, since they no longer serve such an important function, and are not exposed to such severe stresses and strains. The greatly elongated tips of the barbules tend to produce an even and less penetrable surface.

Some of the most interesting adaptations to function are the various ways in which the edge of the wing is made adequate in different places, as described under the heading "Alula." The latter feathers are of morphological interest, being a series

of feathers attached to the bird's thumb, but they are reduced and small. Nevertheless they are very highly specialized to serve a very distinct function. In the elongated lesser coverts of the humerus, known as tertiaries or humerals, we have another instance of a local modification supplied from the nearest and most convenient source. Obviously, unless some special provision were made against it, there would be an opening between the spread wing and the body of the bird which would result in a considerable loss of efficiency. The humerals, which are especially enlarged and modified lesser coverts, growing from a continuation of the series on the humerus, serve this function, successfully bridging the gap which would otherwise occur. In the increasing angle of the shaft of the outer tail feathers we have again an example of the extreme care taken in the fine adjustment of all parts of the plumage to their particular use, since, were this adjustment neglected, the tail would be in a permanently spread condition, unless special muscles were developed and continually used to keep the feathers closed together.

The ordinary contour feathers of the breast and back, serving for warmth and protection and to give an elastic, automatically adjustable surface, do not need, and do not possess, such a highly developed minute structure as do most of the wing and tail feathers, but they are eminently adapted for the purpose they serve. Their insertion at a wide angle with the body of the bird, with a sharp bend in the shaft to bring the interlocking parts of the feather to lie flat on the contour, gives a thick, soft, elastic, warm covering that could hardly be more effective. Where it is necessary for the feathers to lie perfectly smooth, they are not inserted in this way, e.g., on the head. The strong downward arch of the upper tail coverts to make them fit firmly against the base of the tail feathers is also worthy of mention.

No more perfect adaptations to function could be found than the modifications of the ear coverts, eyelashes, and bristles of the head. The ear coverts, by their open structure, are adapted to protect the ear opening from dust and dirt, and at the same time to admit sound waves without interference; the eyelashes are adapted to project out over the eye and protect it as do the hairy eyelashes of mammals, these feathers being made hairlike

in form by the total loss of barbs on the main shaft, which is stiff and straight; and the rictal, loral and supra- and post-orbital bristles are adapted by their coarse, open structure, and lack of soft or superfluous parts, to cover those parts of the face where ordinary contour feathers would be subjected to an undue amount of wear and tear and soiling.

Transmitted June 27, 1913.

LITERATURE CITED

Bonhote, J. L.
1912. On a peculiar type of feather in the water rail. British Birds (London), 5, 42–44, 1 fig. in text.

Headley, F. W.
1912. The flight of birds (London, Witherby & Co.), x + 163, 16 pls., 27 figs. in text.

Nitzsch, C. L.
1867. Pterylography. Trans. from the German, ed. by Sclater, P.L. (London). Ray Soc. Publ., x + 181, 10 pls.

Pycraft, W. P.
1893. On the interlocking of the barbs of feathers. Nat. Sci., 3, 197–203, 6 figs. in text.

Riddle, O.
1908. The cause of the production of "down" and other downlike structures in the plumages of birds. Biol. Bull., 14, 163–175.

Strong, R. M.
1902. The development of color in the definitive feather. Bull. Mus. Comp. Zool. Harvard College, 40, 147–184, 9 pls.

Wray, R. S.
1887. On some points in the morphology of wings of birds. Proc. Zool. Soc. London, 1887, 343–357, pls. 29–32, 2 figs. in text.

EXPLANATION OF PLATES

All figures of feathers of *Circus hudsonius*

PLATE 16

Fig. 1. Branched tip of filoplume, showing terminal barbs and barbules. × 40.

Fig. 2. Base of group of filoplumes, showing method of insertion into fibrous tissue of skin. Note that roots of all are distinct from each other. × 40.

1

2

PLATE 17

Fig. 3. Proximal barbule from middle of inner vane of third primary. Note the stout base, the narrow dorsal recurved edge, the narrow, pointed, ventral lobes, and the distinct nuclei. × 160.

Fig. 4. Distal barbule from middle of inner vane of third primary. Note the short base, the very long tip, the three short, stout, ventral lobes, the four moderate hooklets, and the well-developed barbicels. × 160.

Fig. 5. Proximal barbule from middle of outer vane of third primary proximal to the incision. Note the long, slender base, the narrow dorsal edge, the sawlike ventral lobes, and the single series of well-formed barbicels. × 160.

Fig. 6. Distal barbule from middle of outer vane of third primary, proximal to the incision. Note the general short stout form, long ventral barbicels and hooklets, and rudimentary dorsal barbicels. × 160.

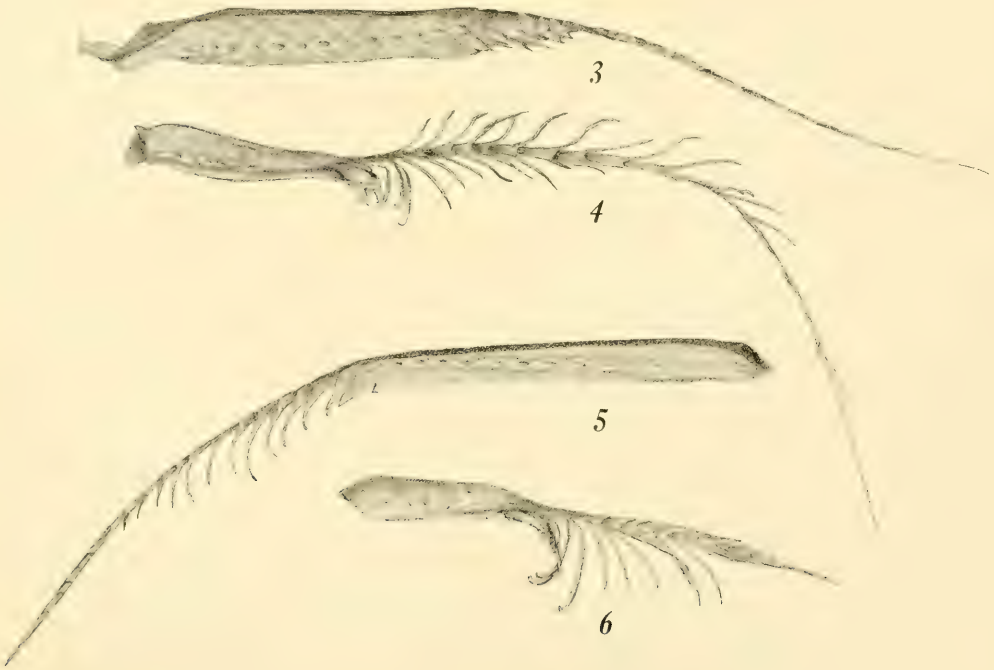

3
4
5
6

PLATE 18

Fig. 7. Proximal barbule from outer vane of first alula feather. Note the stout form, the dorsal teeth, the numerous ventral lobes, and the tapering from basal portion to tip. × 160.

Fig. 8. Distal barbule from outer vane of first alula feather. Note the short, stout form, and the long hooklets and barbicels on the ventral side. × 160.

Fig. 9. Proximal barbule from outer vane of an outer tail feather. Note the moderately stout base, the large, distinct nuclei, the short tip, and the series of blunt projections on the middle third of the ventral edge. × 160.

Fig. 10. Distal barbule from a feather from middle of back. Note the long, slender base, the single ventral lobe, the comparatively weak hooklets, and the barbicels, weak and scattered on the ventral edge, and rudimentary on the dorsal edge. × 160.

Fig. 11. Proximal barbule from a feather from middle of back. Note the slender base, the poorly developed ventral lobes, and the short tip. × 160.

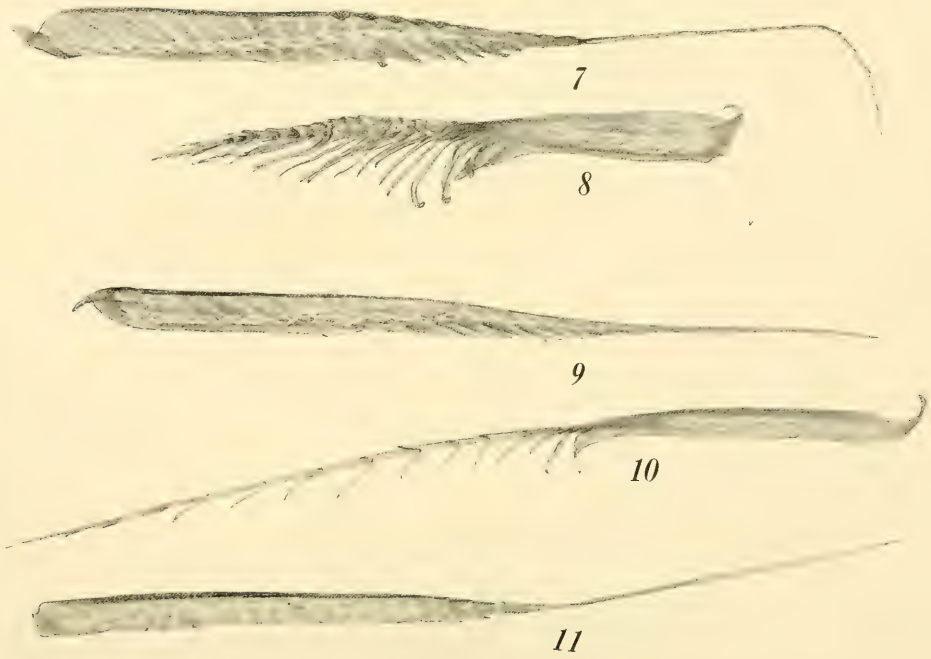

7
8
9
10
11

PLATE 19

Fig. 12. Proximal barbule from a feather from lower belly. Note the long and very slender base, the tip with rudimentary barbicels, and the total lack of ventral lobes. × 160.

Fig. 13. Distal barbule from a feather from lower belly. Note the extremely slender base, the small ventral lobes, the three weak hooklets, and the rudimentary barbicels. × 160.

Fig. 14. Proximal barbule from a feather from facial ruff. Note the small size and lack of ventral lobes. × 160.

Fig. 15. Distal barbule from a feather from facial ruff. Note the small size, the progressively larger hooklets, and the small ventral barbicels. × 160.

Fig. 16. Proximal barbule from a feather from crown of head. Note the small size, the short tip, and the general lack of specialization. × 160.

Fig. 17. Distal barbule from a feather from crown of head. Note the small size, the slender, weak hooklets, and the poorly developed barbicels. × 160.

Fig. 18. Barbule from ear covert. Note the slender undifferentiated form, and the tendency for appearance of weak, rudimentary barbicels. × 160.

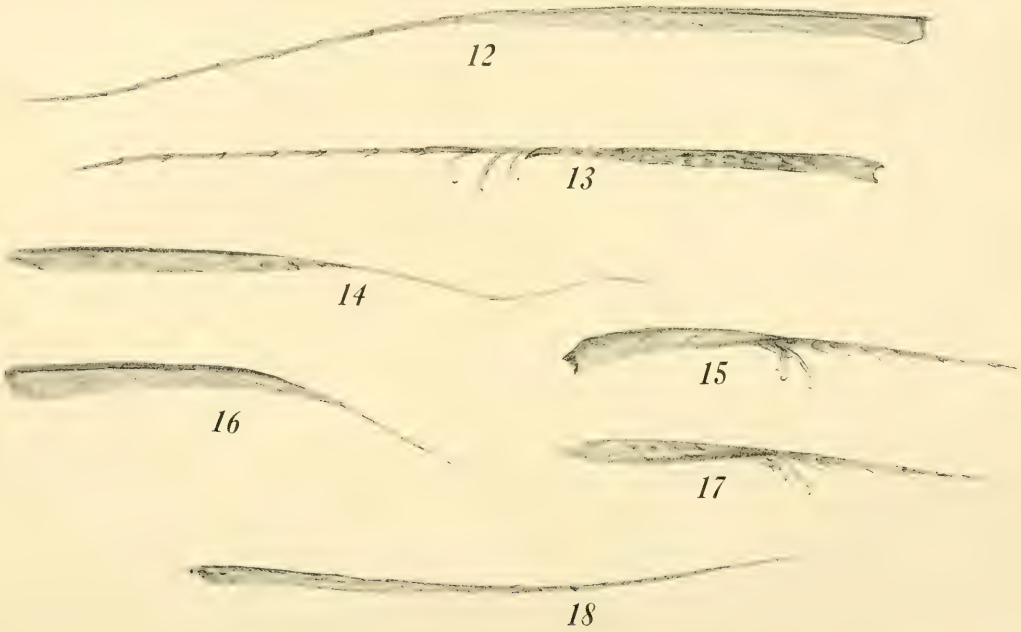

12
13
14
15
16
17
18

PLATE 20

Fig. 19. Supraorbital bristle. Note the stiff naked projection of the shaft, the rather rudimentary barbs, and the aftershaft. × 17.

Fig. 20. Eyelash. Note the rudimentary barbs representing the aftershaft. × 24.

Fig. 21. Portion of barb from lesser wing covert, showing transition from downy filamentous barbules to differentiated proximal and distal barbules. × 34.

19

20

21

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY
Vol. 11, No. 14, pp. 377-510, pls. 21-24, 5 text figs. February 27, 1914

A DETERMINATION OF THE ECONOMIC STATUS OF THE WESTERN MEADOW-LARK (*STURNELLA NEGLECTA*) IN CALIFORNIA

BY
HAROLD CHILD BRYANT

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY

Smithsonian Inst.
MAR 31 1914

UNIVERSITY OF CALIFORNIA PUBLICATIONS

Note.—The University of California Publications are offered in exchange for the publications of learned societies and institutions, universities and libraries. Complete lists of all the publications of the University will be sent upon request. For sample copies, lists of publications or other information, address the Manager of the University Press, Berkeley, California, U. S. A. All matter sent in exchange should be addressed to The Exchange Department, University Library, Berkeley, California, U. S. A.

OTTO HARRASSOWITZ, LEIPZIG.

Agent for the series in American Archaeology and Ethnology, Classical Philology, Education, Modern Philology, Philosophy, Psychology, History.

R. FRIEDLAENDER & SOHN, BERLIN.

Agent for the series in American Archaeology and Ethnology, Botany, Geology, Geography, Mathematics, Pathology, Physiology, Zoology, and Memoirs.

ZOOLOGY.—W. E. Ritter and C. A. Kofoid, Editors. Price per volume, $3.50. Commencing with Volume II, this series contains Contributions from the Laboratory of the Marine Biological Association of San Diego.

Cited as Univ. Calif. Publ. Zool.

Volume 1, 1902-1905, 317 pages, with 28 plates $3.50

Volume 2 (Contributions from the Laboratory of the Marine Biological Association of San Diego), 1904-1906, xvii + 382 pages, with 19 plates $3.50

Volume 3, 1906-1907, 383 pages, with 23 plates $3.50

Volume 4, 1907-1908, 400 pages, with 24 plates $3.50

Volume 5, 1908-1910, 440 pages, with 34 plates $3.50

Vol. 6.

1. (XXIII) On the Weight of Developing Eggs. Part I, The Possible Significance of Such Investigations, by William E. Ritter; Part II, Practicability of the Determinations, by Samuel E. Bailey. Pp. 1-10. October, 1908 ..... .10
2. (XXIV) The Leptomedusae of the San Diego Region, by Harry Beal Torrey. Pp. 11-31, with 11 text-figures. February, 1909 ..... .20
3. (XXV) The Ophiurans of the San Diego Region, by J. F. McClendon. Pp. 33-64, plates 1-6. July, 1909 ..... .30
4. (XXVI) *Halocynthia johnsoni* n. sp.: A comprehensive inquiry as to the extent of law and order that prevails in a single animal species, by Wm. E. Ritter. Pp. 65-114, plates 7-14. November, 1909 ..... .50
5. (XXVII) Three Species of *Cerianthus* from Southern California, by H. B. Torrey and F. L. Kleeberger. Pp. 115-125, 4 text-figures. December, 1909 ..... .10
6. The Life History of *Trypanosoma dimorphon* Dutton & Todd, by Edward Hindle. Pp. 127-144, plates 15-17, 1 text-figure. December, 1909 ..... .50
7. (XXVIII) A Quantitative Study of the Development of the Salpa Chain in *Salpa fusiformis-runcinata*, by Myrtle Elizabeth Johnson. Pp. 145-176. March, 1910 ..... .35
8. A Revision of the Genus *Ceratocorys*, Based on Skeletal Morphology, by Charles Atwood Kofoid. Pp. 177-187. May, 1910 ..... .10
9. (XXIX) Preliminary Report on the Hydrographic Work Carried on by the Marine Biological Station of San Diego, by George F. McEwen. Pp. 189-204; text-figure and map. May, 1910 ..... .15
10. (XXX) Biological Studies on *Corymorpha*. III, Regeneration of Hydranth and Holdfast, by Harry Beal Torrey. Pp. 205-221; 16 text-figures.
11. (XXXI) Note on Geotropism in *Corymorpha*, by Harry Beal Torrey. Pp. 223-224; 1 text-figure.

    Nos 10 and 11 in one cover. August, 1910 ..... .20
12. The Cyclostomatous Bryozoa of the West Coast of North America, by Alice Robertson. Pp. 225-284; plates 18-25. December, 1910 ..... .60
13. Significance of White Markings in Birds of the Order Passeriformes, by Henry Chester Tracy. Pp. 285-312. December, 1910 ..... .25
14. (XXXIII) Third Report on the Copepoda of the San Diego Region, by Calvin Olin Esterly. Pp. 313-352; plates 26-32. February, 1911 ..... .40
15. The Genus *Gyrocotyle*, and Its Significance for Problems of Cestode Structure and Phylogeny, by Edna Earl Watson. Pp. 353-468; plates 33-48. June, 1911 ..... 1.00

    Index, pp. 469-478.

*Roman numbers indicate sequence of the Contributions from the Laboratory of the Marine Biological Association of San Diego.

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY
Vol. 11, No. 14, pp. 377-510, pls. 21-24, 5 text figs. February 27, 1914

A DETERMINATION OF THE ECONOMIC STATUS OF THE WESTERN MEADOWLARK (*STURNELLA NEGLECTA*) IN CALIFORNIA

BY
HAROLD CHILD BRYANT

CONTENTS

PAGE
Preface ... 378
Introduction ... 382
History of methods in economic ornithology ... 389
Investigation of the economic status of the western meadowlark in California ... 395
A comparison of methods in economic ornithology ... 397
The western meadowlark (*Sturnella neglecta*) ... 400
Field investigation ... 401
Abundance ... 402
Nesting habits ... 404
Depredations ... 404
Experiments on captive birds ... 409
Amount of food required ... 410
Time of digestion ... 412
Examination of the stomach contents ... 413
Collection and preservation of material ... 413
Material ... 415
Examination of stomach contents ... 416
Identification of stomach contents ... 420
Food of the western meadowlark in California ... 420
Vegetable food ... 420
Animal food ... 426
Inorganic matter ... 436
Principal articles of diet ... 437

Smithsonian In

PAGE
Examination of feces 437
Quantity of food 440
Capacity for good or evil as evidenced by the number of birds taking different kinds of food 444
Food of nestlings 447
Variation of kind of food 448
Variation in food according to time of year 450
Variation in food habits according to locality 454
Influence of age and sex on quantity of food 455
Combination of field and laboratory work 456
The relation of birds to insect outbreaks 456
Verdict of ranchers as to the value of the western meadowlark 462
A determination of the economic status of the western meadowlark in California 466
Suggestions for the protection of crops 474
Recommendations as to legislation 475
Some interesting side-lights on the investigation 477
Parasitism 477
Malformation 477
Albinism 478
Incubation and moult 478
The effect of systematic destruction on the numbers of meadowlarks 478
Natural death-rate 479
Do protective adaptations of insects protect them from the attack of birds? 480
Availability as a factor in the kind and quantity of food of birds 487
Solved and unsolved problems in economic ornithology 488
Summary 490
Bibliography 494
Explanation of plates 504

PREFACE

The impetus given in late years to the study of the relations of birds to agriculture in the United States is traceable to the extensive work of the United States Bureau of Biological Survey. From the organization of this department of the United States Department of Agriculture, July, 1885, to December 31, 1911, members of the Biological Survey have prepared and published one hundred and thirty-one documents relating wholly or in part

to the food of birds. Notes on the economic status of over four hundred species of native birds and of over fifty species of foreign birds are to be found in these publications. In many cases extended studies have been made of the food of birds by the examination of stomach contents. In no other country has economic ornithology been accorded the attention it has received at the hands of the United States Department of Agriculture.

In a newly settled state like California, where large tracts of land are being brought under cultivation, disturbances of the natural order of bird life arise in two ways. First, the natural food supply of birds is destroyed through cultivation. Second, a new source of food is often supplied by cultivated crops. Hence birds become of great economic importance. The variety of conditions to be found in so large a state as California makes a study of these economic relations of birds complex and difficult. In spite of the need, therefore, of a knowledge of the value of birds, comparatively little work along this line has been done in this state. Until recently two bulletins entitled "Birds of California in Relation to the Fruit Industry," by F. E. L. Beal, published by the U. S. Bureau of Biological Survey, and a few scattered notes in ornithological literature afforded the only published material on the economic relations of birds in California.

Complaints of the depredations of birds in this state have been numerous. The injury to fruit caused by the linnet (*Carpodacus mexicanus frontalis*) is so great that this bird is branded as a pest by the fruit-grower. In recent years grain-growers have complained of damage to sprouting grain caused by western meadowlarks (*Sturnella neglecta*). These birds have been accused, and rightly so, of boring down beside the sprout with their long bills and pulling off the kernel of grain. Ranchers have maintained that in some cases whole fields of grain have had to be reseeded because of the loss occasioned by these birds. In fact, there has developed so much sentiment against the meadowlark that there has been a persistent attempt made at each legislative session to take protection from the bird.

As the western meadowlark is a bird defended by many because of its insectivorous habits, the agitation following the complaints has afforded an exceptional opportunity to deter-

mine scientifically the economic value of this bird by a thorough investigation. Such an investigation has been made possible through the patronage of the California State Fish and Game Commission, which established a research fellowship in the Department of Zoology of the University of California. In January, 1911, I was appointed Fellow in Applied Zoology on the Fish and Game Commission Foundation in the University of California, with instructions to carry on an investigation into the relation of certain California birds to agriculture. The commission assumed the expense and through its deputies furnished the material for stomach examination. The office work and the laboratory work have been carried on in the Zoological Department of the University of California. The investigation has, therefore, been conducted through the co-operation of the State Fish and Game Commission with the University of California.

To the men past and present who have preceded me in this line of work and who have furnished the world with the underlying facts which have established the science of economic ornithology I wish to give due credit, for without their contributions this work must necessarily have been far more elemental. The helpful criticisms and valuable suggestions of Professor Charles A. Kofoid of the University of California, under whose direction the work has been done, have inspired and assisted me in the task. To Dr. Joseph Grinnell, Director of the Museum of Vertebrate Zoology in the University of California, who has often given me of his time to discuss certain features of the work, I owe much. The help also of Mr. E. R. Ong as laboratory assistant, and of Professor C. W. Woodworth, Dr. E. C. Van Dyke, Dr. F. E. Blaisdell, Mr. John Bridwell, Mr. W. L. McAtee, Miss Anna M. Lute and others in the identification of insects and weed seeds has lightened the burden and facilitated this part of the investigation.

Although collections have been made of a number of birds about which complaint has been received (western robin, bicolored red-wing, Brewer blackbird, horned lark, western mourning dove, and roadrunner), yet, because it was the special object of attack, effort has been concentrated on determining the economic status of the western meadowlark.

The investigation has consisted primarily of field investigation, experimentation, and stomach examination. A large part of the field work has been carried on at Lathrop, San Joaquin County, California, a place admirably suited for the work in hand. Duties on the agricultural and horticultural demonstration train, which toured the state in 1911 and 1912 under the auspices of the Department of Agriculture of the University of California and the Southern Pacific Railway Company, have afforded additional opportunity to study conditions from one end of the state to the other.

Economic ornithology is a new science and has hardly progressed further than the stage of preliminary interest and study. As a result practically all of the work attempted thus far has been of the extensive rather than of the intensive sort, and has been made up largely of a study of the food of birds. In this investigation the attempt has been made to improve on past methods and, by determining the food of birds taken in the same locality each month, or twice each month, to furnish reliable evidence as to their food throughout the whole year. A study of the bird in the field, its depredations, and its life-history, has also been made in order that all available evidence might be obtained.

Considerable difficulty has been experienced in that there has been, and now is, a difference of opinion as to the criteria to be used in the determination of the economic status of a bird. The ideas which have been advanced in the past, and even those of the present day, appear to be unsatisfactory, or at least untrustworthy. It seemed, therefore, that a review of past methods, with the addition of such new ones as appeared to be valuable, might prove not only interesting but of considerable value to future workers in the field. A similar lack of information regarding methods of stomach examination has been evident. A detailed account of the method used in this investigation, therefore, seems justified.

The service which birds render to agriculture has doubtless been overemphasized. On the other hand, the position taken by some that birds are of no value as insect and weed-seed destroyers hardly seems justified by the facts. If there be a mis-

conception as to the utility of birds, it is high time we sought to destroy it and to establish truth in its stead.

The economic relations of birds must necessarily become more and more important. As they do so, the extensive study of the past few years will give way to the intensive study necessary to solve the greater problems of the future. Probably no one thing will play a greater part in the conservation of wild life than will this intensive study. Recognition of the economic value of a single bird will stimulate interest in the protection of all.

This work is published, therefore, in the hope not only that the facts and data here presented may be of general interest and of value to future workers in economic ornithology, but that it may be a factor in promoting the conservation of wild life in California, a state which still possesses enough of its original fauna to make its conservation important and eminently desirable.

INTRODUCTION

Doubtless if our knowledge were not so limited we might be able to find a use for most living things. As it is, we designate animals as useful, neutral, or injurious because of their effect on ourselves or our interests. A thorough study of the interrelations of such animals often reverses our original decisions regarding them. Not many years ago insects as a class were called injurious because some of them destroyed certain crops. Today only a part of the insects are considered destructive, and we are yearly finding that others are of neutral or beneficial character.

Not many years ago birds were looked upon either as pests or as marks for the gunner. Today most of them are looked upon as valuable assets of the agriculturist. As science in the past has slowly lifted us to a plane where we study the complex interrelations instead of the single and obvious ones, so in the future we may expect that more and more each form of life will be found to fill a particular niche in its environment better than any contiguous form.

And yet, viewed from the utilitarian standpoint, there is a certain value in classifying organisms as injurious or beneficial. The danger lies not in the classification itself, but in the risk attendant upon a judgment hastily made or one based on circumstantial or partial evidence. Being the dominant form of life on the earth, it is only natural that we measure the usefulness of things by their immediate effect on ourselves or our interests rather than on the whole complex of nature.

An intimate knowledge of the use of wild life is indispensable to sane conservation. Anything known to be useful may justly demand protection. Anything known to be of no utility in nature may justly be accorded destruction. Ignorance has caused the waste characteristic of the past. Knowledge must prevent waste in the future.

What may not seem to be of use today may be of great importance tomorrow. It appears that the economic value of wild life seldom becomes evident until the form becomes extinct, or at least diminished in numbers. It was only a few years ago that fish were so abundant that no attention whatever was paid to their life-histories. Today the study of ichthyology, including fish-hatching, is a necessity, in order that the supply of this kind of food may continue to be available. Not many years ago people believed that there was an inexhaustible supply of game. Today strict game laws and the most careful conservation alone prevent the extinction of many forms.

Fifty years ago the farmer in the east may have lost some grain and corn from the depredations of birds, but he either planted an extra acre or two to make up for the loss or took it as a matter of course. At the present time, however, when we find not only much of the available land under cultivation, but even that cut up into small tracts and men attempting to earn a living on ten or twenty acres instead of on eighty or a hundred, the depredations of birds are more noticeable. The loss of a sack of grain is hardly noticeable in a large field, but let the same amount be lost in a two- or three-acre field and the loss becomes relatively important and very apparent. It is only natural, therefore, that at the present time complaints against birds are more frequent and more insistent.

Depredations probably increase also as the natural food supply of birds is destroyed and they have to rely on the products of civilization. The change of food caused by change in environment sometimes causes an increase in the number of birds of a species, and thus increases the extent of the depredations. Apparently there are a number of birds in California which have directly profited by the change of environment and are increasing in numbers. The linnet, western meadowlark, and mockingbird undoubtedly belong to this class.

As the crops change, and consequently the food supply, we may even expect that in the future the food habits of birds will change. Hence a knowledge of the food habits of birds at the present time may be of far greater value in the future, when such data are needed for comparison.

Whether it is best to destroy certain birds because of their depredations, or to preserve them because of their value as insect or weed-seed destroyers, has become a real problem. There is not a farmer who is not at some time of the year confronted with this problem. In a newly settled country the question as to the value of certain birds is often of grave importance. If nature were not so closely woven together we might easily solve the problem by simply exterminating those birds which cause damage. In the early days this was tried. It is experience that has taught us the danger attendant on the indiscriminate extermination of any form of life.

The problem stated, the next thing to be considered is: How shall it be solved? Observation has proved an unsafe method of determining the true value of a bird. Mere sentiment fails to convince a large number of the class of people deeply interested from actual contact with the problem. The method which has proved the most dependable is a thorough scientific investigation. The problem is complex. It involves a knowledge of the life-history of birds, insects, and plants, a conception of the interaction of organisms, and an appreciation of the accompanying ecological relations.

A scientific investigation as a means of determining the status of a bird presents just as great possibilities as this method has in other fields. In preventive medicine we see the results of

scientific method. The efficiency of the forest service can be attributed to the same methods. If, then, this type of investigation can help us to conserve our health and our forests, it should also lead to the best method of conserving our native birds.

Professor Charles S. Minot has defined the method of science as "the art of making durable, trustworthy records of natural phenomena." He goes on to say: "The method of science is not special or peculiar to it, but only a perfected application of our human resources of observation and reflection—to use the words of von Baer, the great embryologist. To secure reliability the method of science is, first, to record, everything with which it deals, the phenomena themselves and the inferences of the individual investigators, and to record both truly; second, to verify and correlate the personal knowledges until they acquire impersonal validity, which means, in other words, that the conclusions approximate so closely to the absolute truth that we can be safely guided by them." These statements justify the use of scientific method for any modern problem and especially for the problem in hand.

"But putting aside economic and utilitarian considerations, there is to some of us a greater stimulus to solve the problems of nature. With the birds, and the insects and plants upon which they feed, we share a common heritage, and the more we learn of the life of these, our fellow-workers, the nearer we approach solution of the great riddle of the Universe, the mysterious law-abiding scheme of Nature. The book of knowledge to which we add some iota is marred with mystery, superstition and error, but each proved fact cleanses its pages. 'Facts,' says Laing, 'are the spokes of the ladder by which we climb from earth to heaven.'" (See Coward, 1912.)

The labor, time and cost of such an investigation as this is amply justified by the results to be expected. A knowledge of the real economic status of a bird means dollars in the pocket of the rancher, for the destruction of any bird which causes serious damage, or the preservation of any bird that is a benefit, has a direct bearing on the size of the crop raised. Nor is the value to the rancher the only value to be considered, for, as will

be seen, a bird has a certain value to society that cannot be reckoned in dollars and cents.

Some entomologists, seeing in insecticides the only successful control measure against insects, are inclined to minimize the value of such a natural control as birds. True it is that birds apparently do not prevent or entirely control insect outbreaks. for insects continue to ravage crops, no matter what the bird population. However, if a certain number of insects cause a certain amount of damage, it must follow that a diminution of the number of insects causing damage must cause some diminution of the damage done even if it be not proportional. We are justified in saying, therefore, that the fact that birds destroy great numbers of injurious insects shows them to be important agents in contributing to the safety not only of crops, but of all vegetation. Judging from the great numbers of insects destroyed at the time of an insect outbreak, we can safely infer that birds may be instrumental in preventing the appearance of insects in abnormal numbers, by helping to keep the numbers near the normal, which we approximate by the phrase, "the balance of nature."

In this practical age almost everything is viewed from the standpoint of dollars and cents. Hence it is desirable that we study the economic value of birds. There is danger, however, in so doing, for such studies may tend to minimize to a certain degree a value which cannot be expressed in dollars and cents. To say that a meadowlark is worth so many dollars to the rancher each year may obscure its esthetic value.

The strongest opponents of the theory that birds are beneficial often emphasize the esthetic value. The following is a quotation from one of these opponents (Baskett, 1910): "Make their song, beauty, grace and interesting habits a part of our culture—and their preservation part of our ethics, but do not try to foist them on the farmer as an economic asset, for he knows better in many cases. If the soldier can make better marches under the martial influence of the 'spirit-stirring drum' and 'ear-piercing fife,' so can the farmer gather inspiration from the activity and cheerfulness of birds."

One need only point to the place which birds take in art and literature to prove their esthetic value. The inspiration for some of the finest paintings, poems and other pieces of literature has come from a knowledge of bird life. That exhilaration and inward joy awakened with an acquaintanceship with birds has a real value. What mental pictures stay longer with us than do those gained first hand from nature? Those things which make the world more beautiful make it more fit to live in.

Few birds there are that have a greater esthetic value than does the western meadowlark. One reason for this is that it is a conspicuous bird and therefore known to every one. Its song has been pronounced far sweeter than that of its eastern relative. Its plumage and general habits add to its attractiveness. A bird associated with the fields and plains, it adds great interest to the general loneliness and monotony of our great treeless areas. What person traveling along a lonely country road has not been cheered by the bird which stands bobbing on many a fence post and telegraph pole and continually pours forth its "Eh heu wheel'iky, wheel'iky, wheel'iky"? (For the musical notation of the song of the western meadowlark see Allen, 1881.)

The educational value of birds has more utilitarian aspects. Birds teach a code of ethics exceeded only by that of man himself. The fidelity of parents to each other and to their helpless young and the industry, cleanliness, grace, and cheerfulness exemplified by them add much to the finer ideals of life.

The educational and esthetic points of view can even be considered economically. To many, this type of presentation detracts instead of adds. Nevertheless, it is true that the esthetic and educational value of birds has its economic relations. Many a summer resort is chosen because of the abundance of birds in the vicinity, and many a summer vacationist is influenced in his choice of destination by the presence of birds in the vicinity. The value of suburban property is enhanced by the presence of birds. That many a business man has been attracted to certain suburban localities because of the presence of the meadowlark and its song is self-evident.

Carrying this point of view to an extreme has often antagonized certain classes, and herein lies a danger. Yet the facts

here presented can easily be verified. A determination of the status of a bird must include a study of the bird from every point of view. To many city folk the esthetic and educational value of a bird is the more important, for they never see it from any other point of view. Perhaps the rancher is an extremist on one side and the city resident on the other. A modification of the views on both sides is very desirable to a sane appreciation of the value of birds in general and the western meadowlark in particular.

The advance made in investigations of the economic relations of birds since Professor Aughey (1878) studied the relation of birds to the locust ravages in Nebraska up to the present, when government experts give the whole of their time to such inquiries, demonstrates the growth of the science of economic ornithology.

A study of this advance, however, shows that only a beginning has been made. Although we know in general the food habits of our common birds, yet conditions vary so greatly that we cannot definitely predict the food in any given locality. The work thus far has afforded us a general survey of the food habits of birds and in some few instances has given us definite knowledge as to the usual food of certain birds. The thing that economic ornithology has not afforded us as yet is a *detailed study of the food of a particular bird in a given locality throughout the whole year.*

The importance, then, of a thorough knowledge of the economic relations of a bird in addition to its life-history is evident. It has been left to one of the new sciences, economic ornithology, to tell us of these economic relations and to explain the real status of birds. The agitation coincident with the establishment of this science had made known at least five facts:

1. Birds are very largely insectivorous, and as a result are important in keeping the numbers of insects in check.

2. The amount of food required by birds is enormous.

3. Birds often considered injurious are really beneficial, and vice versa.

4. Birds change their food habits and feed on the kind of food most easily obtained.

5. Birds are very important in preserving that balance of nature most suited to the interests of man, and their place cannot be filled by any other class of living things.

These facts are now familiar. They have furnished a basis for a sane protection, have demonstrated the intricacy of the interactions of organisms, and have helped develop the economic view of birds.

Although economic ornithology is fundamentally the study of birds from the standpoint of dollars and cents, and, therefore, includes their use as food, as cage birds, etc., yet emphasis has rightly been placed on the study of the food of birds. As a result, economic ornithology is most often used in a restricted sense and has reference to the study of the food of birds. Great activity is evidenced in this line of work at the present. Not a month passes that there is not some important contribution to economic ornithology, and there is scarcely an entomological report that does not mention the value of birds as insect destroyers. To appreciate the work of the present, however, there must needs be some knowledge of the work of the past. A brief historical review of the subject, with emphasis on the methods used, will furnish this needed information.

HISTORY OF METHODS IN ECONOMIC ORNITHOLOGY

We need only to examine in detail the progress of our sciences to be convinced that there is such a thing as evolution. As we interpret their progress step by step, and thus survey their general trend, it would seem that the development has been of the orthogenetic type. The biological sciences have been a little slower than others in their development, but they are now taking front rank. One of the most marked tendencies to be noted in history is that of a change from the period when biologists drew conclusions from facts gained from observation only to the present period when more intensive study and experimental evidence are demanded.

The period of time previous to 1850 may be termed the primitive period, for during this time we find only an occasional mention of the food habits of birds, the entire time of the workers

in this field having been given over to classification and habit notes. The following period (1850–1865) marks the time when the specialized science of economic ornithology was founded. It was a period of interest and agitation. Before the conclusion of this period the modern methods of investigation were introduced into America by Jenks (1860). The period since 1865 is best considered the modern period—a time when the attempt to reach truth is backed by experimental evidence and the work becomes intensive rather than general. (See Locy, 1908.)

To the first period belong such men as Catesby, Edwards, Forster, Latham, Bartram, Hearne, and Barton—men who took an active interest in natural history and enriched ornithological literature with what observational facts they were able to glean. In the latter part of this first epoch there began a marked tendency to gain more than superficial facts by observation, and so in the writings of Wilson, Audubon, and Baird we find mention of the food of birds. (See Palmer, 1899.)

It was not till 1860 that Jenks (1860) applied scientific method to the study of the food of birds. Previous to this time there had been considerable agitation concerning the value of birds, and many papers dealing with the question appeared in agricultural journals. Le Baron's "Observations of the Birds of Illinois Interesting to the Agriculturist" is a good type. Other writers at this time were Walford, Holmes, Kirkpatrick, Dodge, Allen, Elliott, and Samuels. The hour was ripe, therefore, for economic ornithology really to take a place among the sciences as distinct from ornithology itself. The work carried on by Jenks (1860), Treadwell (1859), Aughey (1878), and Forbes (1880, 1882, 1883, 1903) gave the science its real foundation, and inaugurated the modern methods now well exemplified and used by the United States Bureau of Biological Survey.

At about the same time we find the science getting a start in Europe. Jenks (1860), when introducing the method of stomach examination into the United States, followed Prevost's (1858) method. M. Florent Prevost was evidently the pioneer in Europe. His paper, "A Memoir on the Alimentary Regimen of Birds," presented to the Imperial Zoological Society of Paris in the year 1858, and translated by Jenks in 1859, should still

be considered a classic. In it he presents an original method of stomach examination and draws some very sane conclusions from the results of thirty years' work.

It is interesting to note that this early worker had a vision of the very method which is advocated at the present time, but which has seldom been followed in detail. He says: "It appeared that it would be of interest to gather, at different periods of the year, the stomachs of all birds which it might be possible to procure, to examine the contents, to note down the exact results of this examination, with the date of the observation, and to preserve these pieces in order to form, in time, a collection by means of which one can in the future verify each of the registered facts." He goes on to point out what he had accomplished in thirty years' work and the methods which he used in preserving stomach contents. These methods were: drying and mounting on cards, drying and preserving in a vial, and preserving in alcohol.

His method of examination appears to have been thorough, for he suggests that an "attentive examination," in many cases, made "fragments such as antennae, jaws, lips with their feelers, feet, and often entire heads" give the means of determining the family, genus, and, in some cases, even the species. Following this is a discussion of the results of the work. The tables used are described thus: "To this end I have drawn up a uniform table for all the species of birds; each copy of this table concerns a species whose name figures at the head. It represents a series of columns, of which each bears the title of an alimentary regimen; it is in these columns, and conformably to their title, that I have inscribed both the date of the observation and the indication of the objects found in the stomachs. In fine, each of these tables contains a sufficient number of lines to register observations made during twelve months of the year, and at five different dates in each month."

Early workers in America have often failed to consider the food of a bird for the whole year. They have also failed to take into consideration the fact suggested by Prevost in the following words: "The studies which I have pursued after the method indicated above will establish the fact that the same species of

bird changes its food according to the age and season of the year." Also that "the moment when certain insects inundate a country with individuals without number, . . . coetaneously, this very abundance seems to invite a crowd of different species of animals to feed upon them." It was not till 1882-1885, nearly twenty-five years later, that Forbes clearly pointed out these interrelations between birds and insects.

Prevost concludes: "I am in the course of proving that birds are in general much more useful than injurious to our crops, and that even in respect to the greatest part of the granivorous species the evil which is done to us at certain times is largely compensated by the destruction of insects which they accomplish at other times. It is important, then, that we do not destroy these species, but only divert them from the crops when they injure them. Their destruction would permit, without counterbalance, the development of many species of insects more fatal still to agriculture. The study of the alimentary regimen has furnished me also some information which I believe useful in comprehending the reunions, the separations, and periodical emigrations which are observed so commonly among birds." (See Prevost, 1858, translation by J. W. P. Jenks.)

Since the work of Prevost, economic ornithology has grown rapidly. Germany has probably been most active in the work. Hawks and owls have received the most attention throughout Europe, probably for two reasons. They have been most widely attacked because of their size, and their value is most apparent upon investigation. A number of societies and institutions scattered over the continent are actively engaged in studying the economic status of birds. Chief of these are the Kaiserliche Anstalt für Land- und Forstwirtshaft zu Berlin, Ornithologische Gesellschaft in Bayern, Paris Museum of Natural History, and the Königlich Ungarische Ornithologische Centrale. The names of Berlepsch, Rey, Custer, Rörig (1903), and Hollrung (1906) have become well known as workers in this field in Germany. Rörig is the one man who has attempted a computation of the comparative amounts of food by a weight method. Csiki (1909) and Greschik (1910, 1911) have been the principal workers in Hungary. Their researches have been mainly confined to the birds of prey.

A committee appointed by the British Association for the Advancement of Science is now investigating the feeding habits of British birds by a study of the contents of the crops and gizzards of both adults and nestlings, and by collation of observational evidence, with the object of obtaining precise knowledge of the economic status of many of the commoner birds affecting rural science. Data as to the environmental conditions under which the bird was feeding and the available food supply are obtained with each specimen. All data obtained from the stomach examination are tabulated, and the weight of the bird and the condition and weight of the gizzard contents are recorded.

The United States Department of Agriculture has carried on the most extensive work in economic ornithology ever attempted by one institution. Study along this line was begun in 1885. Since that time over sixty thousand stomachs of birds have been examined, and the results, with the addition of data collected in the field, have been published in more than one hundred and thirty bulletins.

Other investigations have also been conducted. The most extensive work has been done in Illinois by the pioneer economic ornithologist, Professor S. A. Forbes. Massachusetts, Wisconsin, and Pennsylvania have also carried on investigations, the work being done by Forbush (1908), King (1883), and Warren (1888) respectively. Practically every state has been supplied with some literature on the subject by the state university or the agricultural experiment station.

At the third ornithological congress at Paris in 1900, the section of economic ornithology and bird preservation reported in favor of urging all countries and even their governments to take up seriously the subject of the utility or harmfulness of birds as being of the greatest economic importance. It was urged that "inquiries should be instituted on regular business lines, that migratory and non-migratory species alike should be observed during every month of the year and for several years in succession, that the contents of their stomachs should be carefully noted, and lists prepared of their action towards the farmer's crops."

The amount of careful work along these lines which has been done since this time is very encouraging. The last few years

have seen a number of the leading magazines take up the subject of the economic value of bird life, and with illustrated articles they have brought to the attention of many the value of birds to the farmer.

Largely because of their depredations, the demand for an intimate knowledge of the food of birds has become very pressing, and yet it is interesting to note that attention to the economic side of ornithology was not aroused by the depredations of birds, but by the depredations of insects.

A comparison of the methods used up to the present will clearly show the progress which has been made in the science of economic ornithology. Such a comparison is afforded by the following sequence of methods used in determining the economic value of birds:

Sequence of methods used in determining the economic value of birds:

1. Observational notes on the food of birds. (Wilson, 1808-1814; Audubon, 1827–1838.)
2. Critical observational study of the food of birds. (Le Baron, 1855; Holmes, 1857; Weed, 1903.)
3. Examination of the stomach contents of birds. (Jenks, (King, 1883.)
4. Experimental feeding of captive birds. (Treadwell, 1859.)
5. Observation plus stomach examination. (Aughey, 1878; Judd, 1902.)
6. Observation plus stomach examination plus experimentation. (Forbes, 1903; U. S. Biological Survey.)

Similar progress can be noted in the methods used in determining the food of birds. Their sequence has been as follows:

1. Investigation of food with no reference to time or locality. (King, 1883.)
2. Investigation of food at time and locality of depredations. (Forbes, 1903; Wilcox, 1892; Aughey, 1878; Bryant, 1911, 1912d.)
3. Investigation of food according to the month, regardless of exact locality. (Jenks, 1860; Beal, 1907, 1910.)

4. Investigation of food according to the month in the same locality. (Forbes, 1903; Bryant, 1912a.)

5. Investigation of food according to the month in the same locality, with a comparison with many different localities. (See p. 454.)

The determination of the economic status of birds has likewise progressed. The sequence of the criteria used has been as follows:

1. Inferential evidence.
2. Circumstantial evidence.
3. Number of injurious insects eaten.
4. Proportion of percentage volume of injurious, neutral, and beneficial insects and seeds destroyed.
5. Contrast of all harm vs. all good, including knowledge as to life-history.

From these comparisons it can be seen that great progress has been made. To infer that a bird is injurious simply because it is seen in a grain field or orchard, or to brand it as injurious because of circumstantial evidence in the form of grain or fruit found in the stomach, are obsolete methods today. Furthermore, we recognize at the present time that a bird may eat some beneficial insects and still be a valuable bird. Nothing less than a knowledge of the food for the whole year, combined with a knowledge of the life-history of the bird concerned, allowing a balance of all the benefits conferred with all the damage done, meets the requirements of the present.

INVESTIGATION OF THE ECONOMIC STATUS OF THE WESTERN MEADOWLARK IN CALIFORNIA

Interest centered around the meadowlark for some time previous to the institution of an investigation. A rather dormant complaint against the depredations of the meadowlark in sprouting grain fields was brought to a head in a bill (no. 229) introduced by Assemblyman Stuckenbruck of San Joaquin County

into the State Legislature on January 11, 1909. The bill, which proposed to amend section 637 of the penal code of California, passed through the committee, but was refused passage, the vote standing 32 to 28. On the motion to reconsider, the bill was again brought to a vote and passed with a vote of 41 to 28. The Committee on Fish and Game of the Senate reported favorably on the bill, but it was refused passage on a vote of 17 to 12.

In 1911 Assemblyman Stuckenbruck, at the request of his constituents, introduced a similar bill with the proviso that in the counties of Tehama, Butte, Sutter, Sacramento, Yolo, Colusa, Glenn, San Joaquin, Stanislaus, Tulare, and Kings the meadowlark be not included among the birds protected by the act, hoping thus to allay the opposition met from other parts of the state at the former session of the legislature. This bill, being referred to the Committee on Fish and Game, was returned to the Assembly with a majority report in favor of its passage and a minority against its passage. It failed of passage on March 20.

Continued complaints from the farmers and fruit growers of the state have been made to the State Fish and Game Commission regarding the losses to crops caused by the depredations of birds. The commission has been repeatedly urged to take strong measures to avert the damage done. The usual measure urged is that the particular bird in question should be placed on the unprotected list. On the other hand, many scientists and others interested in birds have pointed out the fact that birds confer a great benefit in keeping down the number of injurious insects and weed seeds, and thus they fill a niche in the economy of nature most suited to mankind which is not and can not be filled by any other form of life. Experience has shown that many belonging to the first class have based their complaints on circumstantial or partial evidence or on evidence not sufficiently reasoned out. Furthermore, these complaints have brought out the fact that really very little is known of the food habits of birds of California. Certain it is that a knowledge of the food habits of a bird is necessary to a determination of its economic status. As a result, therefore, the commission thought it wise that legislation should be based on scientific investigation as to the value of birds, and not on circumstantial evidence. Conse-

quently an investigation into the relations of the birds of the state to agricultural and other interests was instituted.

The institution of the investigation was largely due to the interest and energy of Mr. John P. Babcock, Chief Deputy of the California State Fish and Game Commission, 1910–11, and Professor Charles A. Kofoid of the Department of Zoology of the University of California.

A COMPARISON OF METHODS IN ECONOMIC ORNITHOLOGY

The attempt to show the amount of the different kinds of food contained in the stomachs of birds has led to the use of two distinct methods, both of which must be considered valuable, and both of which approximate the end sought. A method introduced by King (1883), and later used by Newstead (1908), gives the total number of birds taking the different kinds of food compared with the total number of stomachs examined. The second method, employed by the United States Biological Survey, depends entirely upon the comparative volume of the different kinds of food found in the stomach, calculated in per cent of total volume and averaged. A third method, in which actual counts of the insects found are made, has been used in a few instances (Mason and Lefroy, 1912; Fisher, 1893). Workers in this field in Great Britain have used the numerical system almost entirely, depending for a criterion upon the number of birds taking a certain kind of food.

Since all of these methods appear to furnish certain information not furnished by the others, a combination of all three methods has been used in this investigation. Dependence is laid on the first method for an idea of the percentage of birds of a species feeding on a particular insect, on the second for an idea of the comparative amounts of the different kinds of food taken by individuals and by the species, and on the third for an idea of the actual numbers of the different elements of food. The counting of weed seeds and insects found in the stomach of a bird is difficult and fruitful of error. Yet the fact that smaller

numbers are always counted than truly exist, owing to the comminuted condition of some, makes it evident that no exaggeration is possible here. Consequently it affords dependable evidence as to the numbers of weed seeds, insects, etc., taken by a bird. On the other hand, the percentage-of-volume method can be depended upon only to furnish an idea of the comparative quantities of the different kinds of food. Personal error in estimating has to be allowed for in this method, for whereas a certain insect might be to the eye of one person ten per cent of the volume, it might represent fifteen per cent to the eye of another.

The furnishing of complete data as to the bird whose stomach is examined (date, locality, kind of field, collector, etc.) should afford information, first, as to the variation in the amount of food taken by birds during the day, month, and year, and second, the food preference of birds in a given locality and in different localities. The record of the exact time of day, the month, and year when the bird was collected furnishes the basis for the first, the record of the habitat, as, for example, the kind of field, orchard, or vineyard, the basis for the second.

An attempt has also been made to improve the method used in determining the economic status of a bird. As has already been pointed out, the economic status of a bird was originally determined by inference. A bird in the grain field must be eating grain and therefore is injurious. Experience has taught that such reasoning is fraught with error. And further experience has taught us that even though a bird may cause considerable damage, yet because of its usefulness as a weed-seed destroyer, as an insect destroyer, or as a bird important in keeping the balance in nature most suited to man, it may be more beneficial than harmful. At one time the total good accomplished by a bird was held to inhere in the number of injurious insects it destroyed. Today, although we still retain this idea, we see a little further and conclude that a bird may be beneficial because it destroys insects (almost all insects being potentially destructive), and not because it chooses a particular class of insects arbitrarily classified as harmful by man.

An attempt has been made to arrive at the average volume of food taken by the meadowlark, by determining the volume

of food contained in a large number of stomachs in cubic centimeters and taking an average volume. This allowed the recording of each stomach as being of average volume, over the average, or below the average.

Identification of the various insects and weed seeds found in the stomachs has been difficult. Help from the experts of the United States Department of Agriculture, from the Department of Entomology of the University of California, and from others has facilitated greatly the identification. Certain field work, embracing studies of the abundance of birds, the depredations of birds, nesting habits, the relation of the birds to insect outbreaks, the kind, amount, and availability of food, and the time of digestion, has afforded needed supplementary information.

In addition to the importance of this investigation to agricultural interests, it has been fruitful of valuable data from the standpoint of science. Although the investigation has been carried on primarily to furnish practical information as to the exact relation of the western meadowlark to agriculture and horticulture, yet no pains have been spared to collect data of purely scientific interest. The importance of a knowledge of life-histories has been emphasized only of late. Information as to the food of any form of life constitutes one of the most far-reaching phases of its life-history. As Forbes (1903) pointed out: "Since the struggle for existence is chiefly a struggle for subsistence, a careful comparative account of the food of various competing species and genera, at different places and seasons and at all ages of the individual, such as has not heretofore been made for any class of animals, cannot fail to throw much light upon the details, causes and effects of this struggle. The flexibility of the food habits of the widely ranging species, the direct effects of normal departures from the usual average of food elements upon the origin of variations, and the general reactions of birds upon their organic environment, are examples of subjects upon which light should be thrown by this investigation."

In this investigation the difference in food habits of the nestling and adult has been clearly demonstrated by the examination of a large number of specimens. The difference in the kind and amount of food taken by the two sexes is made available

for the first time. Field investigation has been fruitful of an increased knowledge of the general habits, nesting habits, abundance, depredations, and distribution of the western meadowlark.

The handling of so large a number of specimens taken from all parts of the state and during each month of the year has furnished information as to variation, albinism, parasitism, and malformation. Critical evidence as to the value of certain so-called protective adaptations of insects has also been afforded. The investigation of the relation of birds to insect outbreaks has emphasized their importance at such times and furnished critical evidence as to the interrelations of these organisms.

THE WESTERN MEADOWLARK (*STURNELLA NEGLECTA*)

In spite of its name, the western meadowlark is not a true lark, but belongs to the family Icteridae along with the blackbirds and orioles. It is easily recognized by its medium size, gray- and brown-streaked back, brilliant yellow throat, black V-shaped collar, and its conspicuous white outer rectrices.

The meadowlark is widely distributed over North America. The eastern meadowlark (*Sturnella magna magna*) differs from the one found in the west in size, color, and song. The western meadowlark is slightly larger than the eastern bird, is paler in color, and has a much richer song. For these reasons the western form is considered a distinct species and is called the western meadowlark (*Sturnella neglecta*).

It is found from Wisconsin, Illinois, Iowa, Texas, etc., west to the Pacific Coast, and from central and western Mexico to British Columbia and western Canada. It is to be found throughout the State of California from sea level to 7000 feet elevation in the mountains.

The western meadowlark is resident throughout the year. A slight altitudinal migration perhaps takes place, governed largely by the available food supply, but usually the bird is to be found in the same general locality throughout the year.

The western meadowlark is a conspicuous bird of treeless areas and a frequenter of meadow, pasture, or uncultivated grass land. Although a poor flyer when compared to some birds, the meadowlark, with its peculiar hovering flight, is possessed of a method of locomotion sufficient for its needs. Its mode of life necessitates but a small amount of flying.

During the fall and winter months meadowlarks gather in flocks of five to fifty or more. During the spring, however, they are seen singly or in pairs. Of a nervous temperament, they are wary and do not often allow of close approach. Both the male and female are good singers. Their cheerful and varied song is sometimes given from mid-air, but more often from a fence post, shrub, or clod.

The western meadowlark appears to be one of the few birds which is profiting by the increased cultivation of land. Alfalfa furnishes particularly good food and cover for the bird, and grain fields are often chosen for a home. With the furnishing of still more good food and cover, combined with the destruction of some of its enemies, this bird may be expected still further to increase in numbers.

The western meadowlark feeds almost exclusively on the ground. It seldom perches in a tree of any kind. The early morning hours are spent in obtaining food, whereas the middle of the day is usually spent quietly hiding in the grass.

The food, composed largely of insects, grain, and weed seeds, is procured not only from the top of the ground, but also by probing beneath the soil and by searching under clods, manure, etc. Alfalfa and grain fields appear to be the favorite feeding grounds of these birds in cultivated districts.

FIELD INVESTIGATION

Next to the knowledge of the food of a bird in determining its economic status is a study of the bird at the scene of action, or, in other words, a knowledge of the habits of the bird. Evidence along this line can be afforded only by field investigation.

Over a month's time was spent at Lathrop, San Joaquin County, California, studying the abundance, feeding habits, nest-

ing habits, depredations, etc., of the western meadowlark. As has been stated, this particular locality was chosen because it afforded not only an abundance of birds, but also a favorable proportion of cultivated and uncultivated land, thus allowing a study of food preference.

The field work carried on can be grouped under three heads: studies of the abundance, of the habits, and of the depredations. Studies of the relations of birds to insects and to insect outbreaks have also been included in the field investigation, but will be discussed in another place. (See p. 456.)

Abundance of the Western Meadowlark

Several findings in connection with the field work have tended to minimize somewhat the depredations of the meadowlark. Perhaps one of the most important is the preference which the bird shows for uncultivated land. Censuses have absolutely demonstrated that, during hours of feeding, western meadowlarks are more abundant in pasture land than in cultivated fields. Evidence as to the abundance of the western meadowlark is also afforded by the censuses.

The following are censuses taken in the vicinity of Lathrop, San Joaquin County, on a two and one-half hour drive:

	Uncultivated (Pasture)	Cultivated (Grain and alfalfa)
February 28, 1912	158	65
May 31, 1912	69	27

These two censuses covered practically the same length of time and the same territory. As the birds were seen in flocks in February, it is only natural that more birds were recorded. May being in the nesting season, the birds were then more widely scattered and not so easily seen. It is apparent that the meadowlark prefers uncultivated land even at the time of feeding. A similar census taken at Acampo, San Joaquin County, during an hour's walk (2–3 P.M.), resulted as follows:

	Number
Orchards, vineyards, and pasture	25
Grain fields	2

Meadowlarks were more abundant in the vicinity of Lathrop than in the vicinity of Acampo. There is very little pasture land in the vicinity of Acampo. This, if not the main reason, is one of the important ones which account for this contrast in abundance. Another contrast in abundance can be noted from the following censuses, two taken at Los Banos, Merced County, July 11, 12, 1912, and the other at Merced, Merced County, July 17, 1912. Those at Los Banos were taken while walking less than five miles, and occupied about four and three hours respectively. The one at Merced was taken while driving about fourteen miles, and occupied the time between 1:30 and 5 o'clock.

Locality	Date	Time	Meadowlarks seen	Average per acre
Los Banos	July 11, 1912	3–4:30	36	1.0
Los Banos	July 12, 1912	2–5:15	67	1.0
Merced	July 17, 1912	1:30:5	23	.1—

It is evident, therefore, that the abundance of this species of bird is largely affected by locality. Probably in the last analysis food supply is the important factor. This brings us to the question: Can the western meadowlark obtain its natural food in cultivated fields as easily as in the uncultivated? If we consider insects as vegetable feeders, then we should expect to find the best insect supply where plant growth was most luxuriant. The cultivation of land destroys much of the natural plant growth, and therefore must diminish the food supply of the insects enough to vary the abundance. Grasshoppers, cutworms, and wireworms can usually be found more abundant in grassy pasture land than in orchards or grain fields. Hence it is a natural consequence that we find meadowlarks frequenting untilled land more often than tilled land.

The censuses taken also demonstrated the fact that meadowlarks were found in the pasture land in greater abundance during the middle of the day than in the morning hours of feeding. During the hotter periods of the day these birds hide in the grass. Open fields are seldom chosen at this time of the day.

Nesting Habits

The nesting season of the western meadowlark lasts from March to August. The nest is a well-concealed one, built of dry grasses usually in grass, alfalfa, or grain fields, in a depression in the ground. A canopy of dry grass stems usually arches the top of the nest and a runway two to five feet long leads to the nest. Ofttimes this runway is the only clue to the location of the nest. The female bird does most of the work of incubation and feeding of the young, while the male acts as a guard. Eggs are usually five and are white, variously marked with brown, purple, and lavender spots and lines.

Work in the spring of 1911 and 1912 substantiated the fact that western meadowlarks usually nest twice each year. The first nesting usually occurs in April and May and the second in July and August. Probably on an average not more than three young are in a brood, although the number of eggs laid is usually five. Second nestings examined usually show an incomplete set of eggs. A preference for pasture land for nesting sites was shown, at least eighty per cent of the nests found being so situated. The time of incubation was found to be twelve to fourteen days. The young stay in the nest but a short time, eight to ten days. Nestlings are exposed to many enemies, such as skunks, weasels, rats, and hawks, and the number of broods successfully reared is less than that of most other birds. That over ten per cent of the nests in most localities are destroyed by predacious animals and birds seems a very conservative estimate.

These facts have an important bearing on the economic relations of the meadowlark. Proximity of breeding grounds to cultivated crops naturally has an influence on the amount of damage done. The rate of reproduction influences the amount of damage, owing to the number of individuals to be expected in any locality.

Depredations of the Western Meadowlark

No small part of the field work has consisted in investigations of the damage caused by the western meadowlark. In most cases the field work has been supplemented with stomach examinations.

The principal complaint lodged against the western meadowlark has been that this bird destroys sprouting grain. The field investigations have proved that this complaint has a real foundation. An interesting side-light on this habit is afforded by a paragraph from Coues's (1874) "Birds of the Northwest": "In April, before pairing, hundreds used to frequent daily the parade ground of Fort Randall, where, as the grass was yet scarcely sprouted, good opportunity was offered of observing their characteristic habit—one not so generally known as it should be, since it is related to the peculiar shape of the bill. The birds may be seen scattered all over the ground, busily tugging at something; and on walking over the scene of their operations, the ground, newly softened by the spring thaw, is seen to be riddled with thousands of little holes, which the birds make in search of food. These holes are quite smooth—not a turning over of the surface of the ground, but a clean boring, like that made by sinking in the end of a light walking stick; just as if the birds inserted the bill and then worked it about until the hole was of sufficient size. Whether they bored at random, or were guided by some sense in finding their prey, and what particular objects they were searching for, I did not ascertain; but the habit was so fixed and so continually persevered in as to attract general attention."

This habit of boring into the ground to obtain sprouting seeds and possibly insects is therefore a habit of old standing, and is not one recently developed.

A careful investigation of a sprouting grain field where meadowlarks are abundant will demonstrate to any one that the western meadowlark pulls sprouting grain. At times the drill row is followed for distances of four to six feet and apparently every sprouted kernel is pulled up (pl. 21, fig. 1). With its long awl-like bill, the meadowlark bores down beside the sprout, grips the kernel and pulls it up. The kernel is occasionally eaten, but more often it is simply crushed in the bill to obtain the milk and then dropped (pl. 21, fig. 2). Consequently stomach examination cannot be relied upon to furnish accurate evidence as to the total amount of grain thus destroyed.

Certain fields examined have given evidence that the deeper furrows made by drills were most frequented by the birds.

Whether this was due to the better cover or to the ease with which the sprouting grain could be obtained it is impossible to state.

Where meadowlarks are very numerous and the field of grain small and isolated, considerable damage results. In some cases such fields have had to be resown. Since the loss of a small patch of grain means far more to the small farmer than does a larger amount of grain to the large rancher, the bird's depredations here are important. The investigations have shown, however, that fields apparently badly damaged by meadowlarks when the grain was sprouting yielded the usual crops at harvest time. This can be accounted for in this way: The birds can succeed in pulling the grain for only a short period of time after it appears above the ground. By the time the second and third leaf appear the plant is well enough rooted so that the loss of the kernel, even if it should be removed, would not injure the plant. Consequently the apparent devastation is largely minimized by the further sprouting of other kernels and the successful survival of the sprouts of many of the kernels removed. A certain amount of thinning may at times indeed be desirable. The lack of uniformity in the thinning accomplished by meadowlarks is, however, an argument against them.

Broadcasted grain, unless harrowed in very deeply, suffers more than drilled grain. It is the universal verdict of the grain ranchers of the state that deeply drilled grain suffers less than the shallowly drilled or the broadcasted grain. Experiments have shown that the greatest yield comes from drilled grain.

The following table is from University of California Publications, Agricultural Experiment Station, Bulletin 211:

Relative Results From Drilled vs. Broadcast Seeding Upon the Yield of Grain

	Average of 22 trials	
	Barley	Wheat
Drilled	70.80	34.85
Broadcast	64.43	31.60
	6.37 bu.	3.25 bu.
Percentage increase	9.9	10.3
Money value	$3.18	$3.12

The proper depth for grain to be planted in sandy soil is three to four inches. If all grain were planted at this depth very little damage would be possible, for meadowlarks are unable to bore more than two and one-half inches at most. Holes measured average about an inch and a half in depth.

Margins of fields bordering pasture land usually suffer most. Ofttimes a noticeable difference in the amount of grain growing along the edges of fields can be attributed to the work of meadowlarks.

Owing to the concentration of large numbers of meadowlarks on a single field, fields of grain planted early suffer most from the depredations of these birds. Grain sown late in the year suffers much less, for insects become available in small numbers and there is less concentration of damage, due to the larger amount of available food.

Meadowlarks are more able to obtain grain planted in sandy soil. Their ability to bore deeply into soil after kernels of grain varies directly with the hardness of the soil. Hard, dry, adobe soil precludes attack. Sandy soil, especially after being softened by a rain, is easily manipulated to advantage.

An apparent preference of the birds for oats has been shown not only by field investigation, but by the complaints of the ranchers also. Probably its availability is a greater factor than any preference shown by the bird. That less damage is possible to wheat and barley because the kernel is more easily removed without damage to the plant is one theory proposed. Certain it is that there is a difference in the damage to adjoining fields of oats and barley.

Beyond an occasional instance of meadowlarks pulling sprouting garden seeds, the only other complaint of importance is that they destroy melons by boring holes in them. Most of the complaint has come from the San Joaquin Valley, and especially from Delano and Pixley, Kern County. Melon growers, although admitting that meadowlarks cause considerable damage to melons, have been unable to demonstrate the actual damage in the field. Opinion is divided as to whether they cause any damage. Some prominent growers affirm they are never troubled. Others complain of a considerable loss. For instance, the names of two

melon growers in the vicinity of Dinuba, Tulare County, were handed in as those of men who were greatly troubled. One returned a verdict of "not guilty," and the other reported that the damage was not very great. All of the growers report that as soon as there are broken melons in the field the birds cease to be troublesome. Apparently the depredations of meadowlarks on melons have been exaggerated.

There is evidence to support the view that meadowlarks bore into the melons to obtain water. Whether or not they are attracted by the sweet taste we cannot say. The placing of water in a field as an experiment would doubtless confirm or disprove this view.

An occasional complaint that meadowlarks are injurious to grapes has been received. Inquiry in grape-growing sections of the state has led to the conclusion that such damage is negligible. A number of birds are destructive to grapes, chief of which are the oriole and grosbeak. Both of these birds are well known as fruit eaters. The meadowlark, on the other hand, seldom turns its attention to fruit of any kind. No damage to grapes caused by the meadowlark has been noted in the field.

Investigations of the damage caused by meadowlarks has led to the following conclusions:

1. The western meadowlark is destructive in sprouting grain fields, because of its habit of drilling down beside the sprout and pulling up the kernel. The amount of damage done is dependent on the particular location, the abundance of the birds, the character of the soil, the time of year, depth and method of planting, and the kind of grain. The damage to oats is greatest, wheat suffers considerable damage, whereas barley suffers but little. Broadcasted grain suffers more than drilled, because not being sowed so deeply it is more easily obtained by meadowlarks. The birds often follow the drill row and pull almost every kernel. Occasionally, where meadowlarks are very numerous and the quantity of grain small, fields have had to be resown. The real amount of damage done has evidently been overestimated, for fields apparently badly damaged have given the average yield later in the year. After the second and third leaf appears on the grain, the bird can do little damage. This fact reduces the

duration of their depredations to less than two weeks, and consequently minimizes the amount of destruction possible. Deep planting and drilling as against broadcasting are important as measures for protecting crops.

2. Damage to other cereals, such as corn and maize, and to fruit is negligible.

3. Investigation of complaints that meadowlarks are destructive to melons has shown that damage caused in this way has been exaggerated. Melon growers, although claiming that the birds cause considerable damage, have often been unable to demonstrate the actual damage in the field.

4. Censuses have demonstrated that the western meadowlark prefers grass land to cultivated land, nearly forty per cent more birds being found in the former.

EXPERIMENTATION ON CAPTIVE BIRDS

Experimentation on captive birds as a means of determining food preference has been suggested by Forbes (1903) and Judd (1901). No doubt such experimentation furnishes considerable evidence as to the food preference of the bird if carried on with proper controls. Thus far this sort of experimentation has not furnished dependable generalization as to what the bird would have taken under natural conditions (McAtee, 1912). This does not mean that better devised and controlled experiments would not furnish dependable evidence.

The difficulty of keeping in cages birds with the temperament of the western meadowlark and the difficulty of procuring for them proper food has prevented the use of feeding experiments in this investigation.

In order properly to estimate the quantity of food consumed daily it has been necessary to determine the time of digestion. It was in this determination, and in the determination of the quantity of food, that experiments on captive birds became of value.

There are four methods of determining the quantity of food required by young birds. First, the quantity of food carried

to the young by the parents may be observed; second, the stomach contents may be examined and the quantity estimated; third, experimental feeding of caged birds may be used; and fourth, the quantity of food may be determined by a daily weighing of nestling birds and of their excreta.

The first method, owing to the difficulty of observing in the field the feeding of the young of so shy a bird as the western meadowlark, has been largely neglected in the interest of the other more practical methods. However, some observations as to the number of trips to the nest made with food have been made. In one instance a female western meadowlark carried food to the nest three times in twenty minutes (6:15–6:45 A.M.). As the presence of the observer caused some nervousness on the part of the parent birds, this cannot be considered the normal rate.

Amount of Food Required by Western Meadowlarks

Stomachs of nestling western meadowlarks examined contained as high as two grams of insect food. Maxima of seven large cutworms, of twelve grasshoppers (three-quarters of an inch in length), and of eight beetles have been found in the stomachs of nestlings. One stomach contained twenty-four ants and parts of a ground beetle. The volume of nestling stomachs and of their capacity in terms of the common elements of food follows:

Volume of average cutworm	.5 c.c.
Volume of average ground beetle	.3
Volume of average grasshopper	.75
Volume of average stomach of ♂ western meadowlark	3.00
Volume of average stomach of ♀ western meadowlark	2.50
Capacity of average ♂ stomach in cutworms	6
Capacity of average ♀ stomach in cutworms	5
Capacity of average ♂ stomach in ground beetles	10
Capacity of average ♀ stomach in ground beetles	8
Capacity of average ♂ stomach in grasshoppers	4
Capacity of average ♀ stomach in grasshoppers	3

A nestling western meadowlark after obtaining no food for three hours was fed twenty-eight small grasshoppers (one-half inch in length), equal in volume to about three cubic centimeters. Another one was fed four grasshoppers (one inch in length), twelve small grasshoppers (one-half inch in length), one robber

fly, one beetle, and five ants. A third one was fed thirty grains of wheat inside of ten minutes.

Weighings of nestling birds demonstrated the fact that they gained very nearly seven grams (0.6 ounce) in weight daily. Solid excreta averages 0.48 gram. The weight of excreta voided during twenty-four hours must be near 3.6 grams, thus making the weight of food required daily over ten grams. This computation does not take into account the weight of excretory products given off through the skin or the weight of carbon dioxide given off through respiration. The ratios of solid, liquid, and gaseous excreta are not known. The tabular results of weighings follow:

Weighings of Nestling Meadowlarks

	Time of weighing		Average weight of 2 western meadowlark nestlings		
Date	Nest No. 1	Nest No. 2	Nest No. 1	Nest No. 2	
May 26	6:00 a.m.	.....	.75 oz.		
May 27	8:30 a.m.	.....	1.25		
May 28	8:40 a.m.	.....	1.50		
May 29	7:15 a.m.	5:45 p.m.	1.75	.75 oz.	.50 oz.
May 30	7:45 a.m.	5:00 p.m.	2.9	1.00	.75
May 31	4:25 p.m.	.....	2.0	.....	.....
June 1	7:30 a.m.	6:30 a.m.	2.25	1.50	1.25
June 3	.....	6:15 a.m.	.....	1.75	1.50

Weight of egg ready to hatch	.135 oz.
Weight of day-old nestling	.25
Weight of eight-day-old nestling	2.50
Weight of average adult	4.00

Although more experiments are necessary to establish the exact gain in weight of nestling birds, yet these experiments have furnished evidence as to the enormous quantities of food consumed by nestling birds. When one considers that there is a gain of about three ounces (93.3 grams) in weight inside of two weeks, and that this added weight must be calculated by the weight of food consumed minus the waste thrown off in the various forms of excreta and expired air, the quantity of food necessary is evident. Not only is enough food needed to maintain energy, but an additional amount to maintain weight increment is demanded during the period of growth. Probably each young

western meadowlark consumes something like five ounces (155.5 grams) of food during the time it remains in the nest. This weight in grasshoppers would mean 311 individuals and in cutworms 415 individuals.

The time of digestion of the western meadowlark was determined by feeding captive juvenile birds and examining the condition of the food at intervals after feeding. The following table gives a summary of the results of these experiments:

Tabular Results of Experiments on the Time of Digestion

Experiment	Time without food	Time between feeding and killing	Food given	Condition of food on examination
1	3¾ hrs.	2 hrs.	4 large grasshoppers (*Camnula pellucida*) 12 small grasshoppers 1 robber fly 1 beetle (*Coniontis* sp.) 5 ants	Finely comminuted and largely digested
2	5¾	3¾	20 grasshoppers (*Camnula pellucida*) 10 ants	About one-quarter of volume remained; all soft parts digested
3	3¼	2	30 kernels wheat	15 kernels left undigested; hulls still undigested
4	3½	2	1 May beetle (*Ligyrus gibbosus*) 1 weevil (*Rhygopsis* sp.) 12 grasshoppers (*Camnula pellucida*)	Only hard parts left in stomach (heads, wing-covers knee joints, etc.)
5	4	5?	28 grasshoppers	Stomach empty

From these data it can be safely concluded that insects are digested in two to four hours and that the stomach is completely emptied every four hours. Beetles and ants, owing to the chitinous parts, remain longer in the stomach than do grasshoppers. Cutworms doubtless are digested much more rapidly. Grain is more difficult to digest than insects and remains in the stomach longer (four to five hours).

These results compare very favorably with the results of similar experiments by other investigators. Experiments carried on by Treadwell (1859), Forbush (1907), and Weed and Dearborn (1903) have demonstrated that birds have a very rapid

digestion, most of them requiring from one to four hours only to digest a meal. All evidence of food had disappeared from the excreta of a crow within two and one-half hours after feeding. Professor Treadwell showed that juvenile robins digested a meal every two to four hours.

All evidence, therefore, points to the fact that four hours can be considered a sufficient period of time to assure the digestion of the stomach contents of a western meadowlark. The contents of the stomach at the time the bird is killed must have been taken within four hours previous to the collection of the bird. The daily consumption must, therefore, be considered about three times the capacity of the bird's stomach. As the birds start each day with an empty stomach and with the additional stimulus of hunger, the greater amount consumed during early morning hours compensates for the smaller amount taken during the middle of the day.

EXAMINATION OF THE STOMACH CONTENTS

Collection and Preservation of Material

Birds in sufficient numbers to furnish reliable data, collected every two weeks during a year, and from over twenty different localities in the state, have been made available through the cooperation of the deputies of the Fish and Game Commission. Each bird was tagged with data as to date, time of day, locality, kind of field or orchard, and collector. Dependable data regarding abundance of food were not available as a general rule. The birds were then preserved in formalin. On the arrival of shipments at the laboratory the stomach (gizzard) was removed and data as to the species and sex of the different birds added. The tag bearing complete data was then wrapped with the stomach in a small cloth, and preserved in ten per cent formalin until microscopically examined.

In determining the localities where collections have been made an attempt was made to select well-settled parts of the state representative of the different agricultural sections. The following instructions were sent to each deputy:

INSTRUCTIONS TO COLLECT BIRDS FOR SCIENTIFIC INVESTIGATION OF THEIR RELATION TO AGRICULTURE

Dear Sir:—

In order to obtain material for our field investigation of the relations of game and other birds to agriculture, we propose to collect specimens of all the field and orchard birds in the State other than quail, ducks, geese, and crows during the first and third week of each month.

We want especially one-half dozen each of meadowlarks, robins, and blackbirds collected during these weeks in grain fields and the same number in vineyards or orchards in sections where there are both. We want, also, two doves from the same section for each of the two weeks mentioned. For the present we will confine our attention to meadowlarks, horned-larks, robins, and blackbirds. Where practicable obtain specimens of each species of your district from the same field or fields of a like character near by, because we wish to show just what they feed upon throughout the year.

As each bird is killed fill out one of the string record tags furnished you, being careful to note the hour, date, character of field, orchard or vineyard, the location and the name of the owners and the nearest post-office. Then securely fasten a tag to each bird. In writing upon the tags use plain lead pencils only, as the preserving fluid will destroy ink and indelible pencil marks.

After filling out the tag, attach it to the bird and then record in a notebook devoted to this work a similar record to the one on the tag.

Upon returning from the field proceed to preserve the specimens as follows: From any drug store purchase a 40 per cent solution of formalin or formaldehyde. Then place in an ordinary two-quart fruit jar one-half pint of the 40 per cent formalin and then fill up that jar with clear water and mark it "Jar No. 1." Then place your specimens in another jar (or jars) and fill it with the liquid from "Jar No. 1," and seal the top to prevent evaporation. Don't place too many specimens in a jar; give them room enough to become thoroughly saturated. Keep the specimens in the solution for at least a week. See that the tag of each specimen is uninjured.

At the end of each month take your specimens from the solution and wrap in a cloth wet from the solution in "Jar No. 1" and place in a thin cracker box or a tight wooden box and ship as hereafter directed, together with a copy of the record from your notebook.

The solution from which you remove your specimens can be used several times, supplying the necessary additional solution from "Jar No. 1."

Recember that birds have no value unless each is securely tagged with a record of the hour, date, etc.; that our work depends absolutely upon the accuracy and reliability of the record. Send separate bills covering your purchase of shot, formaline, jars, traveling and other expenses connected with this work to this office. Do not include them on your regular bills.

The necessary permit to take these birds throughout the year is furnished you herewith.

Inform your local press and others interested just what you are doing and the object we have in making this collection, to wit, investigating the relations of our birds to agriculture, so that there may be no misunderstanding.

Finding that it worked a hardship on the deputies to spend certain days of each month collecting birds, the original instructions were modified as follows:

Our order concerning the collection of non-game birds, for scientific investigation, is hereby modified to permit collecting at *convenient times* instead of during the *first* and *third* weeks of each month. The collection, however, must be distributed evenly so that nearly the same number of specimens are secured in each bi-weekly period.

Under this order we believe the deputies themselves can, while on other duty, take all the specimens needed for our work and thereby greatly reduce expense. In consequence we direct that all special collectors be dismissed and their permits and collecting material taken over by the regular deputies responsible for their engagement.

Material

The accompanying map (fig. A) shows the localities in which collections have been made. The localities from which complete series, that is, birds collected each month of the year, were made, and those localities from which incomplete series were obtained, are both indicated. The attempt was made to have a minimum of six specimens collected each month. In several instances collections of a dozen birds each month were obtained.

In order that the work of 1911 might be verified, collections were continued at Live Oak, Sutter County; Sacramento, Sacramento County; Newman, Stanislaus County; and Salinas, Monterey County, during 1912. This afforded a comparison of the food in two successive years, and has acted as a check on the results obtained the first year.

A total of 2070 stomachs of western meadowlarks has been available for examination, of which number nearly two thousand have been examined and the results tabulated. The largest collection available, composed of one hundred and seventy-five birds, was from Hanford, Kings County. The largest number available taken in a single month was twenty-four.

I.—Table Showing Material Suitable for Stomach Examination

Locality	Collector	Number of meadowlarks	Number of months represented	Numbers taken										
				In grain fields	In orchards	In vineyards	In pasture land	In alfalfa fields	In gardens	In ploughed fields	In bean fields	In beet fields	In corn fields	In miscellaneous fields
Eureka, Humboldt County	W. C. Graham, E. C. Barnes	69	12	37	7	.....	21	.....	.....	.....	.....	.....	.....	4
Anderson, Redding, Sisson, Siskiyou County	J. S. White, A. E. Doney	30	9	9	9	.....	3	4	.....	.....	.....	.....	.....	5
Ukiah, Cummings, Mendocino County	B. H. Miller, Wm. Ray	72	7	32	14	9	.....	12	.....	.....	.....	.....	.....	5
Healdsburg, Sonoma County	H. Lencioni	20	3	20	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Red Bluff, Tehama County	T. W. Birmingham	159	12	82	77	.....	.....	.....	.....	.....	.....	.....	.....	.....
Live Oak, Sutter County	E. D. Ricketts	105	19	98	1	.....	.....	.....	.....	.....	.....	.....	.....	6
Susanville, Plumas County	F. P. Cady	6	1	6	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Grass Valley, Nevada County	R. O'Connor	18	9	16	1	.....	.....	.....	.....	.....	.....	.....	.....	1
Napa, Napa County	W. J. Moore	29	9	13	7	.....	7	.....	.....	.....	.....	.....	2	.....
Sacramento, Sacramento County	Geo. Neale	60	13	22	.....	4	30	3	.....	.....	.....	.....	.....	1
Stockton, Lathrop, San Joaquin County	Geo. Merritt, H. C. Bryant	31	6	18	.....	1	12	.....	.....	.....	.....	.....	.....	.....
San Andreas, Calaveras County	C. W. Getchell	6	1	3	.....	.....	2	.....	.....	1	.....	.....	.....	.....
Pleasanton, Alameda County	E. Downing	44	9	26	.....	14	.....	1	.....	3	.....	.....	.....	.....
Newman, Stanislaus County	J. E. Newsome	147	23	141	.....	.....	6	.....	.....	.....	.....	.....	.....	.....
Los Banos, Merced County	J. M. McSwain, H. C. Bryant	94	6	83	2	2	7	.....	.....	.....	.....	.....	.....	.....

I.—Table Showing Material Suitable for Stomach Examination—*Concluded*

Locality	Collector	Number of meadowlarks	Number of months represented	Numbers taken										
				In grain fields	In orchards	In vineyards	In pasture land	In alfalfa fields	In gardens	In ploughed fields	In bean fields	In beet fields	In corn fields	In miscellaneous fields
Madera,														
Madera County	J. H. Perry	18	2	18	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Fresno,														
Fresno County	S. L. N. Ellis	3	1	3	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Hanford,														
Kings County	E. W. Smalley	184	12	46	30	7	13	88	.....	.....	.....	.....	.....	.....
Hollister,														
San Benito County	C. A. McHenry	67	9	52	1	1	5	.....	.....	.....	.....	.....	.....	8
Salinas,														
Monterey County	F. Shook	50	7	16	14	.....	.....	.....	.....	.....	.....	.....	.....	20
Santa Maria,														
Santa Barbara County	H. J. Abels	19	2	10	2	.....	.....	.....	.....	.....	.....	5	.....	2
Big Pine,														
Inyo County	E. H. Ober	71	12	34	9	7	5	5	10	.....	.....	.....	.....	1
Bakersfield,														
Kern County	A. C. Tibbett	6	1	6	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Ventura,														
Ventura County	J. E. Kuhlman	44	5	17	.....	.....	.....	7	.....	.....	15	5	.....	.....
San Bernardino,														
San Bernardino County	J. A. Vale	110	12	99	.....	11	.....	.....	.....	.....	.....	.....	.....	.....
Riverside,	C. H. Vosburgh,													
Riverside County	J. H. Gyger	117	11	38	2	.....	1	63	.....	.....	.....	.....	.....	13
El Toro,														
Orange County	W. K. Robinson	169	12	92	1	9	43	.....	.....	.....	6	.....	.....	18
San Diego,														
San Diego County	Webb Toms	138	12	73	57	7	.....	.....	.....	.....	.....	.....	.....	1
Imperial,														
Imperial County	G. H. Dexter	18	1	10	.....	.....	.....	6	.....	.....	.....	.....	.....	2
Miscellaneous	H. C. Bryant	16	3	.....	.....	.....	15	.....	.....	.....	.....	.....	.....	1
	Totals	1920		1120	234	72	170	189	10	4	21	10	2	88

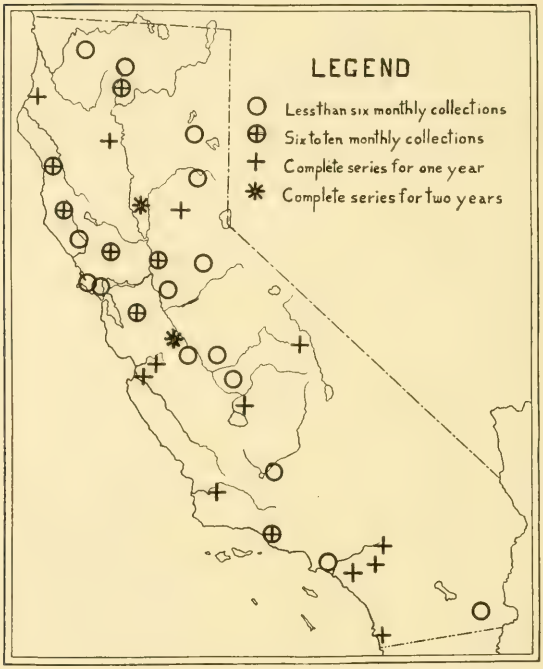


Fig. A.—Map of California showing localities in which collections of western meadowlarks have been made for the purpose of stomach examination. A complete series is a minimum of six birds collected each month in a year.

Table I, pages 416–417, gives a summary of the material available.

Examination of Stomach Contents

On removing the stomach (gizzard) and tag from the cloth, the stomach was carefully cut open, the incision being made with a scissors along the longest axis and through the muscles, starting at the cardiac opening, and the contents emptied upon a glass

plate. Great care was taken to see that every bit of the contents was scraped from the walls of the stomach. A Zeiss binocular was used in examining and determining the material found. Where possible, counts were made of all vegetable and animal elements of food. The amount of mineral matter used as grinding material was computed by a calculation in per cent of the comparative volume.

The comparative volume of each kind of food was calculated in per cent of total volume contained in the stomach examined. In the estimation of apparent volume there is always a personal error. However, since this method is depended upon to furnish evidence as to the comparative amounts and not actual amounts, the personal error is largely distributed in the averages. Parts of insects and weed seeds used in identification were wrapped separately in small pieces of paper to prevent their mixing with the rest of the stomach contents.

Where possible, the heads of insects were used as a safe criterion of the number eaten. In many cases dependence was necessarily placed on an enumeration of the mandibles. In the case of grasshoppers the mandibles are probably retained in the stomach longer than the soft parts, but experiment has shown that the stomach is completely emptied in four hours, so that it is necessary only to give a long enough period of digestion to make such an enumeration dependable. The fact that the mandibles of grasshoppers may be found along the entire length of the digestive tract also supports the view that this criterion is trustworthy. Beetles, bugs, bees, and ants were readily counted, because the heads and thoraces of these insects remain long undigested.

Partly digested grain and weed seeds were computed in percentage volume, but in addition the undigested kernels and seeds were counted.

Owing to the finely comminuted condition of the food to be found in the intestines, that found in the stomach alone was used as evidence of the food taken. The stomach alone gives the best unit of volume. The consideration of the food to be found in the intestines could at best but show evidence as to food for a longer time previous to the death of the bird.

In all cases the stomach contents were preserved in vials, so that verification of the results will be possible at any time. As a rule, the contents have been preserved by drying, but where certain animal matter such as larvae was present the material has been preserved in seventy per cent alcohol.

After each examination the kind and quantity of food was recorded on a stomach blank. Complete data were recorded on larger blanks. Summaries giving the results of the examinations of the different collections were made in the form of tables.

Identification of Stomach Contents

Collections of insects and seeds for comparison were most helpful in identifying the different insects and seeds. Insects and seeds, if in good condition, can be determined at least to the genus by this method. Floating out the wings of certain insects in water and the mounting of other parts in some clearing fluid are methods which have had to be resorted to occasionally.

In the examination of a large series of stomachs it is nearly always possible to obtain a fairly good specimen of an insect which is commonly taken as food, for some bird is usually found which has taken such an insect just before being killed.

Food of the Western Meadowlark in California

The food of the western meadowlark is made up of both vegetable and animal matter. The vegetable food is largely composed of grain and seeds. The animal food is made up largely of insects. The accompanying diagram (fig. B) shows the relative amounts of the different kinds of food taken during the year. A discussion of each kind of food is followed by a statement of the "amount destroyed" and the "economic importance."

Vegetable Food

Grain

Grain forms the largest percentage (seventy-five per cent) of the vegetable food for the year and makes up thirty and eight-tenths per cent of the total food for the year. But a small part (one per cent) of that found in the stomachs has been sprouted.

This was therefore in all probability pulled from the seeded fields. Oats is the grain most often taken. It is not only preferred, but is the most available. Much (about seventy per cent) of that found in the stomachs is wild oats (*Avena fatua*). This oat is so mixed with the tame varieties that part of it must be considered a loss to the rancher, for it makes good feed. Nearly half

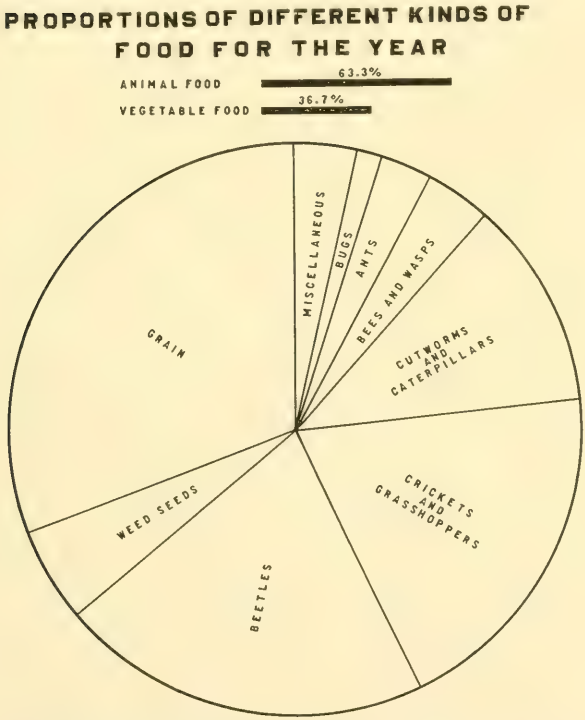


Fig. B.—Diagram showing relative amounts of different kinds of food taken during the year by western meadowlarks.

of all the grain taken by the birds examined was consumed during the three winter months—November, December, and January. It is apparent, therefore, that availability, lack of insect food, and possibly the sprouting condition of the grain are responsible for this. Owing probably to the feeding habits of the bird, mixtures of different grains are seldom found. The stomachs usually contained one kind of grain only.

Barley, because of its greater availability, is more often taken than wheat. The barbs are seldom found in the stomach. One hundred and fifty-five out of one thousand and nine hundred birds had eaten barley.

Wheat is taken less often, probably because it is less available. One would suppose that a grain without the hull would be the more palatable. Field corn (*Zea mays*) was taken by only seven birds out of one thousand nine hundred and twenty, while ten had eaten white milo maize (*Andropogon sorghum*) and other varieties of Egyptian corn.

Quantity destroyed.—During the months of December and January the meadowlark feeds largely on grain. Grain forms nearly thirty-one per cent of the food for the year. Stomachs are often found entirely filled with oats, barley, or wheat. As many as thirty kernels, with enough hulls to account for as many more, have been found in a single stomach (pl. 22, fig. 3). Less than one per cent of the grain found in the stomachs has been sprouted grain. Practically no grain is found in the stomachs during the months of March and July. In that grain is more slowly digested than insects, a smaller volume of grain is probably consumed daily.

Economic importance.—For its destruction of sprouting grain, the western meadowlark justly deserves criticism. In small fields, where the birds are numerous, losses are great. The facts which tend to minimize the damage done are as follows: Much of the grain found in the stomachs is wild oats. Since cultivated oats always contains more or less wild oats in California, it cannot be said that injury does not result from the destruction of the latter. However, much of that eaten must be taken in places where no injury results. All of the grain taken in the months of August, September, and October must be considered

waste grain and of little economic importance. Meadowlarks are not known to attack heads of grain. Whatever field grain is taken is picked up from the ground. Damage done to sprouting grain can result only during a limited period of time (two weeks). After the second leaf appears no damage can result.

Weed Seed

Weed seed evidently forms the principal part of the vegetable diet of this bird where or when grain is not available. The seeds of such weed pests as tarweed, mustard, tumbleweed, Napa thistle, pigweed, amaranth, canary grass, Johnson grass, foxtail, and sunflower are consumed in large quantities. The seeds of such forage plants as the burr-clover and filaree are commonly eaten. The seeds of filaree (*Erodium cicutarium*) form the largest percentage of the weed seeds taken as food.

A stomach has seldom been found completely filled with weed seed, for some sort of grain, especially wild oats, is nearly always available with the weed seeds. Nevertheless during the late fall weed seeds make up a considerable part (twenty per cent) of the diet.

Grass has been occasionally found in the stomachs. Whether or not it was taken intentionally it is impossible to state. Small sprouts from sprouting grain and sprouting seeds have been found in some instances. As a rule the seeds appear to be separated from the large sprouts when eaten. Small pieces of straw and other vegetable fiber found in the stomachs can be classified as rubbish picked up with the food.

There has been a slight complaint that meadowlarks damage sugar beets by feeding on the sprouting seeds. Mr. F. J. McCoy, assistant manager of the Union Sugar Company, Betteravia, California, says on this point: "I have noticed meadowlarks in early spring in our beet fields, but noticed they were feeding on insects." Stomach examination has failed to disclose any beet seeds. The stomachs of birds collected in beet fields have been found filled with insects.

Quantity destroyed.—The maximum consumption of weed seed occurs in October, when nearly one-fourth of the food is made up of this kind of food. Weed seed amounts to five and

three-tenths per cent of the food for the year. Over 150 seeds of filaree (*Erodium* sp.) have been taken from a single stomach. Tarweed, pigweed, tumbleweed, mustard, turkey mullein, Napa thistle, Johnson grass, canary grass, foxtail, sunflower, burr-clover, and nightshade seeds have been found in numbers ranging up to fifty. In some few instances stomachs have been found entirely filled with weed seeds. Western meadowlarks appear to feed upon weed seeds to a considerable extent during the time in which they are available. Most weed seeds do not mature until late summer and fall. After plowing begins they are no longer available in cultivated districts, except along fence rows and in uncultivated fields.

Economic importance.—The destruction of weed seeds must be considered of value to the agriculturist. Weeds even in small numbers take a toll in the grain field. The destruction of weed seeds accomplished by western meadowlarks must help to limit, in some measure, the number of weeds which grow in fields and fence rows the following year. Meadowlarks feeding in grain fields must destroy weed seed that would not otherwise be destroyed. Their habit of feeding on sprouting seeds increases their efficiency as weed-seed destroyers. Seeds eaten are digested. In no case have undigested seeds been found in excrement.

Fruit

No vegetable matter found in the stomachs has been identified as fruit. Grape seeds have been found in a number of cases and there is no doubt that western meadowlarks eat grapes to a slight extent. No serious complaint as to their depredations in this direction has been received. The stomachs of practically all of the birds collected in vineyards have been filled with insects, mostly beetles.

A systematic list of the grain and weed seeds found in the stomachs follows:

Grain
- Oats
- Barley
- Wheat
- Field corn (Zea mays)
- Sorghum (Andropogon sorghum subsp.)

Fruit
- Grape seeds (Vitis sp.)

Weed seed
- Gramineae (Grass family)
  - Andropogon sorghum halepensis. Johnson grass
  - Panicum sp. Panic grass
  - Chaetochloa glauca. Bristly foxtail
  - Chaetochloa viridis. Foxtail
  - Phalaris minor. Small canary grass
  - Avena fatua. Wild oats
  - Bromus sp. Brome grass
  - Lolium temulentum. Darnel
  - Hordeum sp. Barley grass
- Cyperaceae (Sedge family)
  - Carex sp. Sedge
- Polygonaceae (Buckwheat family)
  - Rumex sp. Dock
  - Polygonum sp. Knotweed
- Chenopodiaceae (Goosefoot family)
  - Chenopodium sp. Goosefoot pigweed
- Amarantaceae (Amaranth family)
  - Amaranthus graecizans. Tumbleweed
  - Amaranthus sp. Amaranth
- Portulacaceae (Purslane family)
  - Lewisia sp. Bitter root
- Ranunculaceae (Buttercup family)
  - Ranunculus sp. Buttercup
- Cruciferae (Mustard family)
  - Brassica nigra. Black mustard
  - Brassica sp. Mustard
- Leguminosae (Pea family)
  - Medicago hispida. Burr clover
  - Medicago arabica. Spotted medick
  - Melilotus indica. Yellow melilot
  - Melilotus sp. Sweet clover
  - Trifolium sp. Clover
  - Lupinus sp. Lupine
- Geraniaceae (Geranium family)
  - Erodium cicutarium. Red-stem filaree
  - Erodium sp. Filaree
- Euphorbiaceae (Spurge family)
  - Eremocarpus setigerus. Turkey mullein
- Malvaceae (Mallow family)
  - Sida hederacea. Alkali mallow
- Onagraceae (Evening Primrose family)
  - Oenothera ovata. Golden eggs
- Primulaceae (Primrose family)
  - Anagallis arvensis. Pimpernel

Boraginaceae (Borage family)
Amsinckia intermedia. Amsinckia
Amsinckia sp. Amsinckia
Cynoglossum sp. Hound's tongue
Rubiaceae (Madder family)
Galium sp. Bedstraw
Solanaceae (Nightshade family)
Solanum sp. Nightshade
Compositae (Sunflower family)
Lactuca scariola. Prickly lettuce
Centaurea melitensis. Napa thistle
Centaurea solstitialis. Barnaby's thistle
Carduus sp. Thistle
Hemizonia sp. Tarweed
Helianthus annuus. Common sunflower
Iva axillaris. Ragweed

Economic importance of vegetable food.—The destruction of sprouting grain means a loss of dollars and cents to the rancher. This loss is minimized somewhat by the limited time during which injury is possible and the possibility of protective measures. A much smaller loss can be attributed to the destruction of grain picked up in newly sown fields. Grain on or near the surface of the ground in seeded fields is of doubtful value, as it cannot be depended upon to furnish a strong, healthy plant. Much of the wild oats and some of the tame oats must be considered waste grain or uncultivated grain. Its destruction, in spite of its utility as feed, cannot be considered a direct loss in money value.

Practically all the other seeds destroyed are the seeds of weed pests. The destruction of the seeds of certain forage plants such as filaree could be considered a detriment if they were destroyed in large enough quantities to make any difference in the amount of forage available. This same plant is considered a weed in many places. Any destruction of the seeds of thistles, sunflowers, Johnson grass and like weeds must be considered a benefit.

Animal Food

Coleoptera (Beetles)

The most constant article of diet of the meadowlark consists of beetles. The habitat of the bird would forecast this fact. Ground-beetles (Carabidae, Tenebrionidae), click-beetles (Elate-

ridae), and weevils (Rhynchitidae, Calandridae, Otiorhynchidae) form the largest per cent of this kind of food. Representatives of practically every family of the Coleoptera, however, have been found in the stomachs.

A systematic list of the beetles identified follows:

Cincindelidae
- Cincindela sp.

Carabidae
- Calosoma sp.
- Amara californica Dej.
- Amara conflata Lec.
- Calathus ruficollis Dej.
- Platinus bicolor Lec. (?)

Staphylinidae
- Staphylinus tarsalis Mann.
- Creophilus villosus

Silphidae
- Silpha ramosa Say

Dermestidae
- Dermestes sp.

Erotylidae
- Languria sp.

Histeridae
- Saprinus fimbriatus Lec.

Buprestidae
- ———— ?

Elateridae
- Cardiophorus tenebrosus Lec.
- Anchastus cinereipennis Mann.
- Drasterius livans Lec.
- Drasterius sp.
- Megapenthes aterrimus Horn
- Dolopius lateralis
- Melanotus variolatus Lec.
- Limonius infuscatus Mots.
- Limonius canus Lec.
- Limonius californicus Mann.

Lampyridae
- Telephorus consors Lec.

Malachidae
- Collops marginellus Lec.

Scarabaeidae
- Aphodius subaeneus Lec.
- Aphodius granarius Linn.
- Aphodius rugifrons Horn.
- Hoplia sp.
- Cotalpa ursina Horn
- Ligyrus gibbosus De Greer
- Harpalus pennsylvanicus Dej.
- Agonostoreus maculatus Lec.
- Pterostichus sp.
- Bladycellus rupestris Say
- Anisodactylus dilatatus Dej.
- Anisodactylus sp.

Dytiscidae
- Agabus lugens Lec.

Chrysomelidae
- Glyptoscelis albidus Lec. (?)
- Gastroidea sp.
- Diabrotica soror Lec.
- Disonycha sp.
- Chaetocnema sp.
- Microrhopala melsheimeri Cr.

Tenebrionidae
- Blapstinus gregalus Casey
- Blapstinus rufipes Casey
- Blapstinus elongatus Casey
- Coniontis subpubescens Lec.
- Coniontis viatica Esch.
- Eulabis pubescens Lec.
- Eurymetopon sp.
- Eleodes sp.

Meloidae
- ———— (?)

Otiorhynchidae
- Rhigopsis effracta Lec.
- Rhigopsis sp.
- ———— (?)

Curculionidae
- Sitones californicus Fah.
- Sitones sordidus Lec.
- Lixus perferatus Lec.
- Cleonus virgatus Lec.
- Centrocleonus near angularis Lec.
- Baris cuneipennis Casey
- Baris sp.

Calandridae
- Sphenophorus vomerinus Lec.
- Sphenophorus simplex Lec.
- Sphenophorus sp.

Quantity destroyed.—Beetles are taken every month of the year, and form 21.3 per cent of the total food. Stomachs have often been found filled with nothing but beetles. From twenty to fifty have been found in a single stomach.

Wireworms, the larvae of click-beetles (Elateridae), are taken in large numbers where they are available. As they are less often seen above ground than cutworms, it is only natural that they do not form nearly so large a percentage of the food for the year. The adult click-beetles are also taken (see pl. 24, fig. 8).

Economic importance.—Wireworms are injurious to the roots of plants. Damage by them to garden truck and pasture land is of common occurrence. The ability of the meadowlark to probe into and remove from the soil such insects increases its value as an insect destroyer. The destruction of wireworms must be considered a benefit of considerable importance, especially in meadow and pasture land.

By far the greater number of beetles taken as food are the common ground beetles (Carabidae). These beetles are often classified as beneficial insects, because they are supposed to feed on other injurious insects. Certain ones are predacious and are known to feed on fly and beetle larvae in California. Of the food habits of others little is definitely known, and we are justified in speaking of them as neutral, for they do practically no harm and are not known to do any particular good. Tiger-beetles (Cincindelidae) and carrion-beetles (Staphylinidae), eaten to some extent, must be numbered among the beneficial beetles destroyed. The meadowlark, however, does feed upon many injurious beetles, chief of which are click-beetles (Elateridae), pinacate beetles (*Elcodes* sp.), leaf-beetles (Chrysomelidae), snout-beetles (Otiorhynchidae, Curculionidae), and weevils (Calandridae). Among the leaf-beetles is numbered the destructive California flower-beetle (*Diabrotica soror*). This and other members of the family constitute some of the worst beetle enemies of our crops. Snout-beetles (curculios) and weevils (*Sphenophorus* sp.) are well-known pests of fruit and grain. The continual destruction of large numbers of these injurious beetles must be considered a decided benefit.

Orthoptera (Grasshoppers and Crickets)

Grasshoppers and crickets form a large percentage of the meadowlark's food during the summer and fall, making up as high as eighty-five per cent of the food in August. The species of grasshopper taken is the one most available. Practically all of the species found in the state are doubtless represented in the stomachs. The common cricket (*Gryllus*) and the Jerusalem cricket (*Stenopelmatus* sp.) are common articles of diet. Katydids (Locustidae), being less common insects and having a different habitat, are not taken so often.

A systematic list of the Orthoptera found in the stomachs follows:

Gryllidae
- Gryllus integer Scud.
- Gryllus pennsylvanicus Burm.

Locustidae
- (?) Macrocentrum sp.
- Conocephalus acutalus Scud.
- Stenopelmatus irregularis Brun.
- Stenopelmatus sp.

Acridiidae
- Cedipodinae
  - Camnula pellucida Scud.
  - Arphia sp.
  - Dissosteira spurcata Saus.
  - Conozoa behrensi Saus.
- Acridiinae
  - Oedaleonotus enigma Scud.
  - Melanoplus devastator Scud.
  - Melanoplus differentialis Uhler
  - (?) Melanoplus uniformis Scud.

Fulgoridae
- (?) Labia minor

Quantity destroyed.—Next to beetles, grasshoppers form the most important article of diet. Nearly fifteen per cent of the food for the year is made up of these insects. Parts of as many as twenty-six large grasshoppers (one inch or over in length) and fifty-eight small grasshoppers (one-half inch in length) have been found in a single stomach. The maximum amount of this food is taken in June, July, and August, the birds feeding almost exclusively on these insects during these months. The state over, some grasshoppers are taken by the meadowlarks every month in the year. The quantity taken closely parallels the abundance of these insects.

Crickets as well as grasshoppers are relished by the meadowlark. As many as fifteen pairs of mandibles have been taken from a single stomach, showing that at least fifteen common black

crickets (*Gryllus pennsylvanicus*) had been eaten within four hours by that particular bird. Five per cent of the food for the year is made up of crickets. Wood crickets, better known as Jerusalem crickets (*Stenopelmatus* sp.), being less abundant than the common cricket, are less often taken as food.

Economic importance.—Grasshoppers can be classed as injurious insects. The extent of their damage can be traced to their abundance rather than to the presence of any particular kind of grasshopper. The species which most often become abundant enough to cause serious losses in this state are the differential grasshopper (*Melanoplus differentialis*), the pale-winged grasshopper (*Melanoplus uniformis*), the devastating grasshopper (*Melanoplus devastator*), and the valley grasshopper (*Oedaleonotus enigma*). All of these grasshoppers are destroyed in great numbers by the meadowlark. The more abundant these insects become, the more do these birds turn their attention to this kind of food. Where grasshoppers are abundant, meadowlarks have been found to average as high as fifty grasshoppers a day. (See Bryant, 1912d.) As a grasshopper destroyer, the meadowlark is unequaled by any other bird unless it be the blackbird, and then only because of greater numbers of blackbirds. As grasshopper outbreaks continue to ravage certain parts of the state each year, the meadowlark performs a service to agriculture that can hardly be overestimated, in that it helps to keep the insects down to normal numbers, so that losses do not result, and prevents greater losses by taking a greater toll at the time of an outbreak.

Crickets are usually classed as injurious insects. The degree of injury, as with the grasshoppers, depends largely upon their abundance. Since the species of crickets fed upon by the meadowlark feed almost entirely upon plants and are often destructive to grain, their destruction is to be desired by the rancher. This is especially the case with the Jerusalem cricket, which is very destructive to potatoes.

Lepidoptera (*Butterflies and Moths*)

The general law that birds do not eat butterflies to any great extent appears to hold good in the case of the western meadowlark. (See p. 481). However, the following dependable obser-

vation made by Mr. John G. Tyler of Fresno, California, also furnishes evidence of the fact that butterflies are occasionally, at least, destroyed. "While strolling along the road east of this city the writer noticed a field of alfalfa that was infested with yellow butterflies. A nearer approach revealed the presence of several meadowlarks, and I was so fortunate as to see one of these birds seize a butterfly and make way with it. I am not prepared to say that the victim was actually swallowed, but it was certainly captured and killed."

The larvae of butterflies and moths are common articles of diet. Cutworms and caterpillars form ten per cent of the food for the year, reaching a maximum in May and June, when they amount to nearly a third of the meadowlark's food.

Even hairy caterpillars do not escape destruction. In one instance the larva of the mourning-cloak butterfly (*Euvanessa antiopa*) has been found in the stomach. Smaller hairy caterpillars are of common occurrence. Both the larva and pupa of the sphinx moth have been taken from stomachs. Pupae do not form so important a part of the diet as do the larvae.

The only Lepidoptera positively identified follow:

LEPIDOPTERA (BUTTERFLIES AND MOTHS)

Noctuidae
- Peridromia sp.
- ——— (?)
- ——— (?)

Nymphalidae
- Eugonia californica (Boisd.)
- Euvanessa antiopa (Linn.)
- (?) Papilio sp.

Sphingidae
- (?) Phlegethontius sp.

Quantity destroyed.—Cutworms and caterpillars form about twelve per cent of the food for the year. The maximum quantity is taken in the months of March and April, when almost half of the food taken is made up of these insects. Many of the stomachs contained as many as twenty large cutworms or caterpillars. One bird collected at Red Bluff, Tehama County, contained sixty-six cutworms and over thirty small beetles (pl. 23, fig. 5).

Economic importance.—Cutworms and army worms can be classed as two very important pests in California. Garden truck and even trees are sometimes defoliated when these insects become numerous. The depredations of the grape cutworm are only too well known in the state. Caterpillars are vegetable feeders and are always classed as injurious. The destruction of these pests in very large quantities by the western meadowlark must cause a direct saving to the rancher and fruit grower.

Hemiptera (*Bugs*)

Stink-bugs (Pentatomidae) appear to be relished in spite of their excretions, for they are taken in large numbers. Squash-bugs (*Anasa* sp.) have been found in only a few instances. Negro-bugs (*Corimelaena*) form the only other important Hemiptera taken. Cicadas appear to be relished and often caught. Two stomachs have contained aphids (*Aphis brassicae*). The following Hemiptera have been identified:

Hemiptera (Bugs)

Jassidae	Coreidae
———— ?	Corizus sp.
Aphidae	Alydus pliosulus
Aphis brassicae Linn.	Anasa sp.
Membracidae	Pentatomidae
Stictocephala franciscana Stal.	Podisus pallens Stal.
Cicadidae	Podisus sp.
Platypedia areolata Uhl.	Euschistus conspersus Uhl.
Platypedia minor Uhl.	Euschistus servus Say
Reduviidae	Corimelaenidae
———— ?	Corimelaena sp.

Quantity destroyed.—The commonest true bugs destroyed by western meadowlarks are stink-bugs (Pentatomidae), negro-bugs (Cormelaenidae), leafhoppers (Jassidae), and cicada flies (Cicadidae). They form nearly two per cent of the food for the year. As many as twenty stink-bugs have been taken from a single

stomach. Negro-bugs are not taken in such large numbers, nor are they so abundant. Two stomachs have been found almost filled with leafhoppers, and many others contained two to ten of these insects. Cicadas, near relatives of the eastern seventeen-year locust, are occasionally taken, probably as often as they are available. Bugs form over three per cent of the food for the year.

Economic importance.—Most stink-bugs are vegetable feeders and occasionally give trouble. Negro-bugs are troublesome on berries. In the destruction of these insects the western meadowlark is also conferring a benefit. Leafhoppers are injurious to plants, because they secure their food by sucking the juice of the plant. Any destruction of leafhoppers, however small, is of value. The cicada in California is not abundant enough to be of economic importance. It lays its eggs in the sapwood of plants and trees. Since these insects, if they became abundant, would cause trouble as does the seventeen-year locust of the east, their destruction is to be looked upon with favor.

Hymenoptera (Ants, Bees, and Wasps)

Ants appear to be taken irrespective of size or kind, for they are to be found from the smallest to the largest. The common red and black ants (*Messor, Pogonomyrmex*), field ants (*Formica*), and carpenter ants (*Camponotus*) are most abundant in the stomachs.

Ichneumon flies are taken in considerable numbers. Bees and wasps form a less percentage of the food made up of Hymenoptera. In but one or two cases was a bee definitely identified as a honey bee (*Apis mellifera*). Solitary bees (*Chrysis*) and even bumblebees (*Bombus californicus*) have been found. Cow-killers (Mutillidae) are occasionally eaten, although it has commonly been supposed that they were well protected from attack by their sting, hairy covering, and warning coloration.

For several reasons the Hymenoptera have been very difficult to identify. The finely comminuted condition of the insects has proved an almost insurmountable difficulty. The following only have been identified:

Hymenoptera (Ants, Bees, and Wasps)

Ichneumonidae
——————— ?
——————— ?
——————— ?
——————— ?
Mutillidae
Sphaerothalma californica
Sphaerothalma aureola
Apidae
(?) Apis mellifera
Bombidae
Bombus californicus Smith
Chrysididae
Chrysis sp.
Vespidae
Polistes aurifer Sauss.
Polistes minor Beauv.
Sphegidae
Ammophila sp.
Formicidae
Formacinae
Camponotus sp.
Formica sp.
Dolichoderinae
Tapinoma sessile Say
Myrmicinae
Messor andrei Mayr.
Pogonomyrmex californicus Buckley
Pogonomyrmex sp.

Quantity destroyed.—Bees and wasps form 3.6 per cent of the yearly food. In no case have ichneumon flies, which are valuable parasitic insects, been taken in numbers, five being the maximum found in a single stomach. Their rapid flight probably prevents a greater toll being taken. Ants are often eaten in large quantities and form over two per cent of the food for the year. It is not an uncommon occurrence to find a stomach almost filled with ants. Over one hundred have been found in a single stomach.

Economic importance.—Most bees and wasps are considered beneficial insects. Ants are either injurious or neutral; few are beneficial. In the destruction of ichneumon flies the western meadowlark is destroying a valuable parasitic insect. The destruction of bees and wasps must also be reckoned as a count against the bird. However, the small numbers destroyed minimize greatly the real and the possible damage done. The destruction of most kinds of ants makes little difference one way or the other, owing to their abundance and scavenger habits.

Diptera (*Flies*)

A few members of the family Muscidae, a few flower-flies (*Eristalis* sp.) and crane-flies (*Tipula* sp.) and the pupae of syrphid flies (*Syrphus*) are the only representatives of the Diptera which have been found in the stomachs of western meadowlarks. The following have been identified:

DIPTERA

Eristalis tenax	Lucilia caesar L.
Tachina sp.	Musca sp.
Syrphus sp. ?	Tipula sp.

Quantity destroyed.—Flies do not constitute any important percentage (about one per cent) of the food for the year and when found have been in small numbers. A few green bottle-flies and other members of the same family are eaten, as are also flower-flies and drone-flies. Birds collected at El Toro, Orange County, during 1911 had eaten large numbers of the pupae of flower-flies (*Syrphus* sp.). Crane-flies (*Tipula* sp.) are not taken as often as it would seem they would be from their abundance. Evidence is at hand, however, that western meadowlarks feed largely on the larvae when they become abundant. Mr. W. M. Hughes of Madera, Madera County, has made the following report: "When I visited the tract of land affected, I found myriads of blackbirds and thousands of meadowlarks on the ground making small holes into the ground at the roots of the plants and taking out the worm. Several hundred acres of fine crop was destroyed before the birds collected in numbers sufficient to destroy the pest." The outbreak referred to was in the vicinity of Minturn, Madera County, in 1909. Several hundred acres of barley were destroyed by crane-fly larvae at this time.

Economic importance.—In spite of the fact that the larvae feed upon decaying matter, most flies are considered pests because some of them carry germs of disease. Green bottle-flies are disease carriers. The larvae of flower-flies feed upon plant lice and hence are considered beneficial. The larvae of crane-flies, on the other hand, are destructive to vegetation. The small numbers of flies taken and the fact that injurious as well as beneficial forms are eaten make the destruction of Diptera by meadowlarks of little consequence.

Arachnida (*Spiders*)

Quantity destroyed.—Spiders and their egg-cases form less than one per cent of the food for the year. Most of the spiders taken are grass spiders (Agalenidae) and daddy-long-legs (Pha-

langidae), the commonest of those found in pastures. In no instance have more than two spiders been taken from the same stomach.

Economic importance.—Spiders should be considered as doubtfully beneficial or of neutral value to the agriculturist, in spite of the fact that they feed largely on insects. As a rule spiders are not abundant enough to be of great economic importance. Their destruction at the hands of the meadowlark is of no consequence, as the resulting effect on insect life is so small.

Miscellaneous Animal Food

Miscellaneous articles of diet form three and one-half per cent of the food for the year. The common sow-bug (*Porcellio scaber*) is the commonest crustacean found in stomachs. Two birds had eaten snails. Two birds from San Diego had each taken a scorpion. But few earthworms have been found in the stomachs. Centipedes (*Scolopendra* sp.) and millipedes (*Julus*) appear to form a constant part of the diet. They are evidently taken regularly where available. Two birds had eaten ant-lions (*Myrmeleon* sp.).

Quantity destroyed.—Centipedes, millipedes, scorpions, ant-lions, and sow-bugs may be considered oddities in the diet. Their slight availability may account in some measure for the small numbers taken by the western meadowlark.

Economic importance.—Of these miscellaneous elements in the diet, only millipedes and sow-bugs can be considered injurious. Centipedes are usually considered beneficial, scorpions injurious, and ant-lions of neutral value. None of these forms is taken in sufficient quantity to make their destruction either an injury or a benefit.

Inorganic Matter

Pebbles, used for grinding the food, make up the inorganic matter found in the stomachs. White and red pebbles, probably because of their conspicuousness, predominate. Pebbles appear to be necessary as an aid to the digestion of grain, but much less necessary for the digestion of insects. Pebbles are nearly always

found with grain and weed seed, but seldom with insect food. Doubtless the chitinous parts of the insects largely take their place.

Two nestlings and two adults contained parts of egg-shells. It is a well-known fact that birds often eat the broken shells after the young have hatched. In one instance, at least, the parent birds had fed the young on the shells.

Principal Articles of Diet

The kinds of food forming a definite part of the food of the western meadowlark for the year are as follows:

Vegetable		Animal	
Grain	30.8%	Coleoptera	21.3%
Weed seed	5.3	Orthoptera	20.3
Miscellaneous	.6	Lepidoptera	12.2
		Hemiptera	1.7
		Hymenoptera	5.6
		Diptera	.1
		Arachnida	.2
		Miscellaneous insects	1.9

Examination of Feces

Other than stomach examination, the examination of feces would appear to give the best evidence as to the food of birds. That a considerable amount of knowledge concerning the food of meadowlarks can be obtained in this way is evidenced by the fact that the examination of feces of meadowlarks collected June 15, 1912, in the Berkeley Hills showed the following: Thorax of spider, heads of ants, mandibles and other parts of grasshoppers, wing covers and mandibles of beetles and pubescence from wild oats.

The examination of some feces collected from nestling birds at Lathrop, San Joaquin County, showed that these same hard parts passed through the digestive tract undigested. Consequently this affords a practical method of determining the kind of food taken. Its value as a means of determining the amount of food is much less, for only the more resistant parts can be found.

II.—Average Percentage-Volumes of the Different Kinds of Food of the Western Meadowlark

County	Year	Number of birds	Number of months	Grain	Weed seed	Beetles (Coleoptera)	Crickets	Grasshoppers	Jerusalem crickets (*Stenopelmatus* sp.)	Cutworms and caterpillars	Bugs (Hemiptera)	Bees and wasps (Hymenoptera)	Ants	Spiders (Arachnida)	Miscellaneous	Total animal food	Total vegetable food
Humboldt	1911	69	10	30.5	.7	36.9	.8	9.7	.....	15.5	.2	2.7	.5	.8	1.2	68.6	31.4
Siskiyou	1911	30	8	28.4	1.6	28.4	.6	12.9	.2	16.2	3.4	3.9	.9	.2	2.8	69.6	30.4
Mendocino	1911	72	7	36.7	4.0	26.2	1.0	15.3	.9	6.6	2.5	5.0	.3	.4	.6	59.3	40.7
Sonoma	1911	20	3	45.8	4.9	7.3	1.4	22.2	1.0	15.4	.....	.....	.2	.....	1.3	48.9	51.1
Tehama	1911	159	12	25.5	10.6	8.4	.3	28.1	.....	15.4	2.5	1.5	3.6	.2	.....	65.0	35.0
Sutter	1911	63	11	46.3	9.1	7.1	.6	27.3	.....	6.4	7.6	4.2	.4	.2	.....	49.3	50.7
Sutter	1912	42	7	25.8	6.2	22.0	13.8	8.0	.....	9.4	2.0	4.7	.7	1.2	4.9	66.1	33.9
Plumas	1911	3	1	95.0	.....	5.0	.....	.....	.....	.....	.....	.....	.....	.....	.....	5.0	95.0
Nevada	1911	18	2	73.9	7.1	7.5	.....	2.0	2.5	6.6	.1	.....	.....	.....	.....	18.9	81.1
Napa	1911	29	8	53.8	7.9	10.8	2.9	4.5	.8	8.6	.6	1.2	1.4	.....	2.6	40.2	59.8
Sacramento	1911	24	6	15.2	13.4	29.0	.3	20.3	.....	26.9	1.1	1.9	.8	.2	.4	70.9	29.1
Sacramento	1912	60	7	44.4	2.3	24.0	8.1	2.4	1.1	14.7	.....	1.2	.4	.1	.6	53.2	46.8
San Joaquin	1911	31	6	9.6	2.7	21.4	18.1	18.0	.5	19.4	.1	.6	3.9	.05	1.6	87.3	12.7
Calaveras	1911	6	1	.....	8.7	21.5	.....	.....	.....	7.5	1.5	54.5	4.5	.....	1.7	90.8	9.2
Alameda	1911	4	9	41.0	11.5	14.7	2.7	7.5	.3	14.1	.3	2.7	.5	.5	2.9	45.8	54.2
Stanislaus	1911	75	12	38.4	7.8	8.5	5.9	27.5	.5	3.7	5.3	.4	.4	.1	.2	53.5	46.5
Stanislaus	1912	72	11	32.3	2.0	9.9	5.7	42.4	.....	1.7	1.3	.6	3.0	.1	.8	65.7	34.2
Merced	1911	94	6	3.9	.1	35.2	10.1	25.2	.06	9.9	1.7	3.3	5.4	.5	3.6	95.7	4.3

II.—Average Percentage-Volumes of the Different Kinds of Food of the Western Meadowlark—*Concluded*

County	Year	Number of birds	Number of months	Grain	Weed seed	Beetles (Coleoptera)	Crickets	Grasshoppers	Jerusalem crickets (*Stenopelmatus* sp.)	Cutworms and caterpillars	Bugs (Hemiptera)	Bees and wasps (Hymenoptera)	Ants	Spiders (Arachnida)	Miscellaneous	Total animal food	Total vegetable food
Madera	1911	18	1	12.5	.....	59.5	3.1	.5	3.8	7.6	.....	1.1	5.1	.....	6.2	90.3	9.7
Fresno	1911	3	1	.	.....	31.3	29.3	8.0	.....	.....	.....	8.0	15.0	.....	8.3	99.0	1.0
Kings	1911	184	11	9.3	27.6	19.0	.6	16.7	2.1	11.4	1.1	1.2	2.6	.1	6.7	60.8	39.2
San Benito	1911	67	9	49.5	.3	18.8	18.2	7.0	.....	.5	1.5	1.6	.4	.3	1.1	49.8	50.2
Monterey	1911	50	7	47.8	2.7	6.0	7.7	24.9	5.1	.9	10.5	1.3	.3	.5	3.3	48.2	51.8
Santa Barbara	1911	19	2	27.1	.05	45.2	3.9	3.4	.7	6.4	3.3	3.3	.4	.8	5.5	72.8	27.2
Inyo	1911	71	12	12.7	24.0	25.9	.9	19.3	.1	7.3	1.9	1.0	5.2	.04	2.9	63.0	37.0
Kern	1911	6	1	.1	.....	36.3	.....	8.3	.....	47.3	.5	.6	.8	.....	5.8	99.9	.1
Ventura	1911	44	6	36.9	3.5	28.4	4.0	.....	.1	4.1	.....	1.2	.2	.....	6.6	39.5	60.5
San Bernardino	1911	110	12	26.9	6.5	27.6	1.2	7.4	.9	18.4	3.1	3.8	.7	.2	2.5	67.9	32.1
Riverside	1911	117	12	35.4	3.1	27.1	.4	13.0	4.5	24.0	1.7	1.7	5.7	.1	.....	61.9	38.1
Orange	1911	169	12	31.1	.9	6.7	2.7	41.9	3.7	7.3	1.8	.9	.5	.2	2.5	69.8	30.2
San Diego	1911	138	12	43.4	2.6	19.2	4.5	7.5	2.2	7.8	4.4	1.3	1.2	.2	4.7	53.2	46.8
Imperial	1911	18	1	8.1	. . .	13.0	11.1	20	.....	59.6	.3	.5	. . .	.....	5.0	93.0	7.0
Miscellaneous	1911	16	. . .	.....	.	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	. . .	. . .
Totals and averages	1920			30.8	5.3	21.3	5.2	14.2	.9	12.2	1.7	3.6	2.0	.2	2.6	63.3	36.7

Quantity of Food

Three methods may be used in estimating the quantity of food in a bird's stomach. First, the articles found may be counted; second, they may be weighed; or third, they may be estimated by volume.

The first method, although important as giving an idea of the bird's economic value by showing the number of injurious insects or seeds destroyed, fails to take into account the difference in size of the different articles, and does not show the relative amounts of each kind. The second method has been generally disregarded because of its impracticability. The third or volumetric method allows of a balance of the inequalities of size, and best portrays "the ratios each element bears to the others."

By the numerical method, fifty ants would be placed against, say, six ground-beetles. A computation made by the percentage-by-volume method would doubtless show that these two kinds of food represented only three and twenty-six per cent, respectively, of the whole food. Hence the idea furnished in the first case (a ratio of 50 to 6) is a misleading one. Numbers of one insect cannot be balanced against the numbers of another insect. As each bird of the same species has a certain average stomach capacity, the ratio of each element to this average capacity gives the most accurate idea of the relative proportions of each kind of food.

Although the first and last methods have been those most often used heretofore, the second presents certain advantages (e.g., mathematical accuracy) which should not be overlooked. A combination of the numerical and the percentage-by-volume method has been used in the present work. The number of birds taking the different kinds of food offers further evidence as to their capacity for good or ill.

McAtee (1912) has pointed out that statements of numbers of individuals in stomachs has an interest in direct proportion to the bigness of the number. Believing this to be largely true, the maximum number of individuals found in the stomachs has here received emphasis. These maximum numbers should not be considered as averages.

It does not seem fair to compare the food of a species of bird of small size with that of one of large size without taking into account the bird's capacity. The degree of injury or benefit is largely dependent on the total amount consumed. In this investigation measurements in cubic centimeters of the stomach contents of a number of western meadowlarks have allowed the computation of the average stomach capacity. For male birds this average capacity is three cubic centimeters; for female birds it is two and one-half cubic centimeters. The average capacity is two and three-fourths cubic centimeters.

This method allows of some interesting computations of the capacity for good or harm of the western meadowlark. If there are twelve meadowlarks to the square mile, as there are in many places, these birds demand over one hundred cubic centimeters of food daily. This capacity, estimated in grain, means 2200 kernels, in grasshoppers 150 average-sized individuals, in cutworms 125 individuals, in ground-beetles 300, in ants 2500. As digestion is constantly going on, much larger numbers are in reality taken, as is evidenced by a count of the insects in a stomach. These numbers, therefore, are not even a minimum.

As pointed out (p. 412), the results of the experiments showed that meadowlarks must completely digest a meal inside of four hours. It was also found that grain takes longer to digest than do insects. Thus it can be seen that the food found in the stomach at any one time does not represent the total amount of food taken daily, but only about a third part of that consumed daily. Owing to the slower digestion of grain, the amount found in a stomach must represent more nearly one-half of the daily requirement.

Taking an average capacity of two and three-quarters cubic centimeters and considering that each bird fills its stomach at least three times a day, one hundred western meadowlarks must consume near a liter, or about a quart of food each day. If the food be grain it can be seen that the amount of destruction is considerable; if the food be insects it can be seen that meadowlarks take a large daily toll of insects. The same type of computation shows that a single western meadowlark must consume six pounds of food a year.

Some idea of the average numbers of the common insects, grain, and weed seeds destroyed at each meal by western meadowlarks can be obtained from the following tables, which were computed from the results of stomach examination of birds collected in Sacramento and Stockton, California. The average for the day is three times that for each meal.

Number of Common Insects, Grain and Weed Seeds Destroyed by Western Meadowlarks Collected at Sacramento, California

February to April, inclusive

	Grain	Weed seeds	Beetles	Cutworms and caterpillars	Grasshoppers	Bugs	Ants, bees, and wasps	Spiders
1		61	6	8				
2				71				
3	3		6	5				
4			10	12			1	
5		1	4					
6			8					
7			5					
8			3	1				
9	2	2	5	16				
10				7				
11		3	5	3				
12		3						
13		3	2					
14		7	2					
Totals	5	80	56	113			1	
Av. per bird	3	6	4	8				

September to November, inclusive

	Grain	Weed seeds	Beetles	Cutworms and caterpillars	Grasshoppers	Bugs	Ants, bees, and wasps	Spiders
1		60	2	1	1			
2		61			1			
3		155	1	1	2		1	
4	1	65	4		2	2	6	1
5	2	37	8	22	2	5	1	
6		3			11			
7		200	2		1		2	
8		93	2					
9	25	80						
10		180	2	1			1	
11		15	1		10		1	
Totals	28	949	22	25	30	7	12	1
Av. per bird	2.5	86.2	2	2.2	2.6	.6	1	

NUMBER OF INSECTS TAKEN BY WESTERN MEADOWLARKS AT STOCKTON, SAN JOAQUIN COUNTY, CALIFORNIA

Number of birds	Date	Grain	Weed seed	Beetles	Crickets	Grasshoppers	Cutworms	Hemiptera	Hymenoptera	Ants	Animal	Vegetable
15	March-June, 1912	6	25	88	52	88	68	4	7	4	311	31
	Av. per bird	.4	1.6	5.8	3.4	5.8	4.5	.2	.4	.2	20	2.0
	Av. per bird per day	1.2	4.8	17.4	10.2	17.4	13.5	.6	1.2	.6	60.0	6.0

Few people have any realization of the great quantities of insects consumed by birds. For instance, if we consider that there is an average of one meadowlark to every two acres of available land for cultivation (11,000,000 acres) in the Sacramento and San Joaquin valleys and that each pair of birds raises an average of four young, each one of which averages one ounce in weight while in the nest and consumes half its own weight of food each day, it takes over 343½ tons of insect food each day to feed the young birds in the great valleys alone. The increased consumption of insect food due to nestling birds comes at a time when insects are most numerous, and so is instrumental in helping to prevent an undue increase of insects. As insects become injurious only when in maximum numbers, this increased consumption by birds is doubly important.

A conservative estimate of the approximate amount of the different kinds of food consumed by the average meadowlark in California during a year is as follows:

Grain	1¾ lbs.
Weed seed	½
Insects	2¾
Total	6

The fact that the western meadowlark eats both animal and vegetable food is a point in its favor. If it were exclusively insectivorous the bird could not exist in such large numbers because of the lack of insect food during part of the year. The consequent destruction of insect life would therefore be much smaller.

Certain species of birds when hungry will not only fill the stomach, but will continue eating until the gullet is also filled. This is often found to be the case with linnets and bicolored blackbirds. In no case, however, has the gullet of a western meadowlark been found well filled with food. At the most, the last insect taken before the bird was collected has been found in the lower part of the gullet.

Capacity for Good or Evil as Evidenced by the Number of Birds Taking the Different Items of Food

The percentage-volume method of estimating the proportion of the different kinds of food taken by a bird gives us the best idea of the relative importance of the different kinds of food in the diet of a given bird. However, the frequency of occurrence of the different items in the food, shown by a statement of the number of birds taking each item, furnishes additional evidence as to the capacity of a species for good or ill. The number of birds taking a certain kind of insect food can be regarded as an approximate index of the availability of that kind of food, and to a much less extent as an index of food preference if we consider insects as being evenly distributed and birds as being but slightly influenced by psychological processes. A nearer approximation can be obtained by multiplying the number of birds by the number of insects taken. In such a computation the number of insects taken is considered, as well as the number of birds taking the different elements of food. By this method the index of availability of crickets at Live Oak, Sutter County, was four in 1911, whereas this index was 6902 at Hollister, San Benito County, in the same year. By the same method of calculation the index of availability of grasshoppers was 2162 at Live Oak and but 1541 at Hollister. In the first case crickets were 1670 times as available at Hollister as at Live Oak, and grasshoppers 1.4 times more available at Live Oak than at Hollister. The following table gives a comparison of availability of the commoner insects as evidenced by indices of availability. Preference is here classed as a factor in availability.

III.—WESTERN MEADOWLARKS—NUMBERS AND PERCENTAGES OF BIRDS TAKING DIFFERENT KINDS OF FOOD

Total number examined 1920

	Oats	Barley	Wheat	Corn	Sorghum	Beans	Weed seeds	Grape seeds	Grass	Beetles	Crickets	Grasshoppers	Jerusalem crickets	Cutworms and caterpillars
Number of birds taking	670	155	112	7	8	5	488	18	25	1444	239	587	100	516
Percentage of birds taking	34.7	8.	5.8	.3	.4	.2	25.	.9	1.3	75.2	12.4	30.5	5.2	26.8

	Wireworms	Bugs (Hemiptera)	Cicadas	Ants	Bees and wasps	Ichneumons	Butterflies	Pupae	Flies	Fly larvae	Crane flies	Spiders	Spider egg cases	Centipeds	Millipeds	Sow bugs
Number of birds taking	8	259	15	322	370	25	9	76	33	15	5	72	25	6	8	10
Percentage of birds taking	.4	13.4	.7	16.7	19.2	1.3	.4	3.9	1.1	.7	.2	3.7	1.3	.3	.4	.5

V.—ACTUAL NUMBERS AND PERCENTAGES OF THE DIFFERENT KINDS OF FOOD TAKEN BY ADULT AND JUVENAL MEADOWLARKS

Number of birds		Grain	Weed seeds	Beetles	Crickets	Grasshoppers	Jerusalem crickets	Cutworms and caterpillars	Bugs	Bees and wasps	Ants	Spiders	Miscellaneous	Animal food	Vegetable food
50	Actual numbers taken by adults	11	15	210	16	210	1	50	80	11	49	9	......	......	......
50	Actual numbers taken by juveniles	......	14	207	26	263	3	92	71	27	73	......	......	......	......
50	Percentages taken by adults	2.8	.9	24.8	2.6	45.5	1.8	9.2	8.3	1.4	1.8	1.3	3.6	96.1	3.9
50	Percentages taken by juveniles	3.0	.3	20.7	2.9	38.8	1.2	17.6	5.0	2.0	4.6	......	6.1	95.7	4.3

Indices of Availability of Common Insects Eaten by Western Meadowlarks

Locality	No. of birds	Beetles	Cut-worms	Grass-hoppers	Crickets	Bugs	Bees and wasps	Ants
Live Oak, Sutter Co.	60	1,775	288	2,162	4	533	78	18
Hollister, San Benita Co.	60	4,307	7	1,492	6,680	197	265	35

The most available and the most popular food of the western meadowlark, if it may be judged by the frequency with which it has been found in the stomachs, is beetles. Seventy-five per cent of all the stomachs examined contained beetles (Coleoptera). Vegetable food in the form of oats is next in order of frequency, thirty-four per cent of the meadowlarks examined having taken oats as food. Grasshoppers, cutworms and caterpillars, and weed seeds were found in thirty per cent, twenty-six per cent, and twenty-five per cent respectively of the stomachs examined.

The accompanying table gives a summary of the number of times each article of diet was taken and the percentage of each article in the diet of the species. Attention should be called to the fact that a very large percentage (seventy per cent) of the birds taking oats took wild oats (*Avena fatua*) instead of the tame varieties. Consequently not more than ten per cent of the birds examined had taken cultivated varieties of oats.

Although the percentages showing the proportionate number of times each kind of food is taken to the number of birds examined differs from the percentages showing the proportionate volume of each kind of food, yet they parallel each other to a considerable extent. The accompanying table, giving only the principal articles of diet, shows this parallelism in the percentages.

IV.—Percentage-Volume and Percentage of Western Meadowlarks Taking Different Elements of Food

	Grain	Weed seed	Beetles	Crickets	Grasshoppers	Bugs (Hemiptera)	Ants	Bees and wasps	Flies (Diptera)	(Arachnida) Spiders
Percentage-volume ..	30.1	9.9	17.0	3.5	18.0	3.1	3.0	4.0	.1	.2
Percentage of birds taking	46.0	25.0	75.2	12.4	30.5	13.4	16.7	19.2	1.1	3.7

Food of Nestlings

Three methods are available for determining the food of nestlings; first, the rate of feeding may be determined by watching the number of trips made to the nest by the adult birds while feeding the young; second, the young birds may be made to disgorge their food; or third, the bird may be killed and the food in the digestive tract examined. The first method has not been used with any great degree of success because of the difficulty in approaching near enough to the nest to observe the feeding. The western meadowlark does not become accustomed to an intruder so easily as do other birds. The food observed in the bills of adult birds carrying food to their young has most often been cutworms or grasshoppers. One female bird, while feeding, persistently flew into an oat field and returned each time with cutworms. Another female bird was seen to catch three or four grasshoppers in her bill, and then fly to the nest.

Examination of the digestive tract of nestling birds has shown that they are fed very largely on cutworms, grasshoppers, and ground-beetles. The stomachs of two nestlings obtained from the same nest contained egg-shells. This is not an unusual occurrence, for nestling birds of other species are fed on the egg-shells. In no case was grain found in the stomachs, and in only a few cases were weed seeds found. Young birds doubtless need a larger quantity of food than adults. In almost every case the stomachs were average full or over. This means that each stomach contained nearly three cubic centimeters of food. Since it has been shown that young birds need over one-half their own weight of food each day, the birds when hatched must consume about one-fourth of an ounce a day, and when ready to fly about two ounces.

This increased consumption of insects due to the demands of young birds comes at a time when there are growing crops which need protection and when insects are most numerous, thus emphasizing the value of birds as balancers. The fact that meadowlarks show a greater preference for certain kinds of food while feeding the young enlarges their sphere of usefulness.

In spite of the fact that a certain amount of grain and weed seed is available, young nestling birds are fed almost entirely

on insects. It would seem, therefore, that there is a certain preference for insect food shown at this time of the year. It is a well-known fact that many adult birds which feed on weed seeds feed their young almost entirely on insects. It seems safe to say, therefore, that the western meadowlark, when feeding the young, turns its attention to insects.

The accompanying table (Table V, p. 445) gives a comparison of the food of fifty juvenile and fifty adult western meadowlarks.

Variation in Kind of Food

The kind of food taken by the western meadowlark is dependent upon two *cycles*, the individual cycle and the environmental cycle.

The individual cycle includes such factors as individual taste, time of feeding, and the preference for a particular locality. In fact, all of the factors which depend upon the individual tastes or habits of the bird are grouped here. Whether an individual bird has a particular taste for a certain insect, it is impossible to determine without experiment. Since we find different individuals showing different characteristics, we can safely infer that each individual may show a slight preference for one kind of food above another. Then, too, the time during which the bird feeds has some effect upon the availability of certain kinds of food, so that we should naturally expect that the kind of food would be governed to some extent by the time the bird chooses for feeding. The particular locality frequented by the bird must also influence the kind of food taken. The food of a bird feeding entirely in a grain field would certainly show a slight variation from that taken by one living entirely in a pasture.

The environmental cycle takes into account the changes in the availability of insects and seeds, due to seasonal and climatic conditions. The maximum supply of weed seed is available during September and October. The maximum supply of insects is apparently available during May and June. Even the cultivation of land has much to do with the availability of certain kinds of food. Many weed seeds are easily obtained during September and October, which, after plowing begins, are hidden

beneath the soil and so made unavailable. This helps to explain why birds feed so largely on grain during the winter months. Grain is far more available in cultivated districts at this time than weed seed.

In some localities even a daily cycle may be noted. Certain insects appear in larger numbers after the sun has warmed up the soil. Certain insects, such as cutworms, are found in greater abundance before sunrise. Thus we might naturally expect that birds collected early in the morning would have taken a larger percentage of cutworms than birds collected later in the day. Stomach examination has substantiated this as a fact.

The kinds of crops raised in any particular locality must also influence the kinds of food taken, for it changes their availability. For instance, the stomachs of several meadowlarks contained Egyptian corn and milo maize. Where this crop is raised to any extent the meadowlark doubtless occasionally turns its attention to this type of grain. In other localities where only oats and barley are grown these grains are the only ones available.

VI.—Percentages of Food of Meadowlarks Taken in Alfalfa Fields in the Vicinity of Hanford, California

	Animal matter	Vegetable matter	Number cutworms	Per cent cutworms	Number beetles	Per cent beetles	Miscellaneous
1	100	.....	3	50	4	15	1 potato-bug
2	96	4	2	30	7	46	1 potato-bug, 1 bee
3	100	.....	25	80	9	20	
4	98	2	.....	.....	1	6	1 potato-bug
5	100	.....	5	65	2	12	1 fly, 3 ants
6	96	4	19	76	6	20	
7	100	.....	9	60	7	20	10 ants
8	88	12	23	75	4	10	1 fly
9	85	15	1	10	7	75	
10	94	6	21	83	2	8	1 pupa
11	100	.....	2	80	2	20	
12	100	.....	1	16	10	76	1 fly
13	100	.....	4	55	6	20	17 small flies
14	100	.....	4	85	3	15	
15	17	83	2	10	1	4	1 ant
16	100	.....	8	60	5	14	1 cricket, 2 ant-lions
Totals and averages	92.1	7.9	129	52.1	76	24.3	16.1

Stomach examination has clearly demonstrated the fact that birds collected in alfalfa fields consume much larger quantities of cutworms and caterpillars than birds collected in grain fields in the same general locality. The following table computed after the examination of sixteen stomachs of meadowlarks collected in alfalfa fields in the vicinity of Hanford, Kings County, California, clearly brings out the increased percentage of cutworms and caterpillars in the food taken by birds in such fields. Another table showing a comparison of the food of thirty-four birds collected in the above locality, but in different kinds of fields, brings out the same point.

VII.—Comparison of Food Taken by Western Meadowlarks Collected in Alfalfa Fields, Grain Fields, Orchards, and Vineyards

Averages of nine birds per month collected in March, April, and May, 1911, at Hanford, Kings County, California

Kind of field	Per cent animal food	Per cent vegetable food	Average number of beetles	Per cent beetles	Average number of cutworms and caterpillars	Per cent cutworms and caterpillars
Alfalfa	95.9	4.1	5.1	24.1	11.2	61.4
Grain	99.4	.6	9.4	58.5	1.8	21.0
Orchard	98.3	1.7	4.8	31.7	6.5	55.7
Vineyard	78.3	21.7	.1	5.0	7.0	42.0

Variation of Food According to Time of Year

Abundant data have allowed a comparison of the food of the western meadowlark by the hour, day, week, month, and year. Little change in *kind* of food can be noted from one time of day to another unless birds were taken in different localities. Nevertheless, the *quantity* of food found in the stomachs varies with the time of day. The maximum is found about nine o'clock in the morning, and the minimum from one to two o'clock in the afternoon. The same can be said of the food from day to day. A comparison of the food from week to week, however, shows considerable change.

The change from week to week (and the same can be said of the change from month to month) closely parallels the availability of the different articles of diet. Weed seed and waste grain are nearly always available during September or October.

Yet if enough grasshoppers and ground-beetles are available, the birds evidently take these in preference, for stomachs are more often found filled with insects than with weed seeds. The accompanying diagrams illustrate the great change in food habits from one time of year to another. It will be noted in each instance that the food of the western meadowlark is made up largely of insects during the spring and summer months and largely of grain and weed seeds during the fall and winter months. It is needless to point out that this parallels the availability of insect food, and to a less extent the availability of vegetable food. In that the percentage of animal food for the year is greater than the percentage of vegetable food, and since some insect is nearly always found in stomachs filled with grain

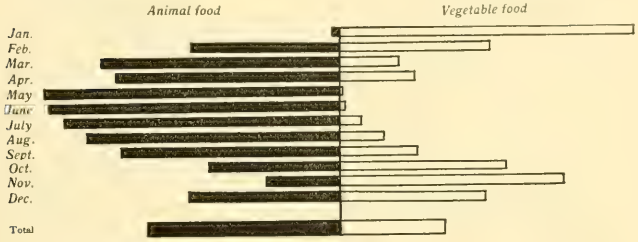


Fig. C.—Diagram showing change of food habits of the western meadowlark from month to month. Note that the maximum consumption of animal food is to be found in May, June, and July, and the minimum, corresponding with the maximum of vegetable food, in January and February. Computed from the results of stomach examinations of an average of twelve birds taken each month of the year at Red Bluff, Tehama County, California.

and weed seeds, whereas grain and weed seeds are far less often found in stomachs filled with insects, it seems safe to say that animal food is preferred and vegetable food is used as a makeshift.

The diagram showing the food of western meadowlarks collected in the vicinity of Red Bluff (fig. C) illustrates this preference for insects. Ninety per cent of the birds examined were

collected in grain fields, and yet the only time when they turned to grain was in the winter, when the numbers of insects were at a minimum. Evidently grain fields furnish an abundant supply of animal food during most of the year. The maximum consumption of animal food is in June and the minimum in January. The minimum of animal food corresponds necessarily to the maximum in vegetable food.

The diagram showing the proportion of the two kinds of food of birds taken in the vicinity of San Bernardino (fig. D) lacks some of the inaccuracies to be noted in the former diagram. The maximum consumption of animal food is in April instead of May, due to the difference in climatic conditions. The birds taken in this locality, although collected largely in grain fields, consumed an unusually large proportion of animal food during 1911, more, in fact, than any other series of birds collected in southern California.

The amounts of food taken by meadowlarks collected every two weeks at Newman, Stanislaus County (fig. E), also clearly brings out the change in food habits from one part of the year to another.

The averages of the different kinds of food for the year do not change greatly from one year to another. The time of year when the different kinds of food reach a maximum in the diet

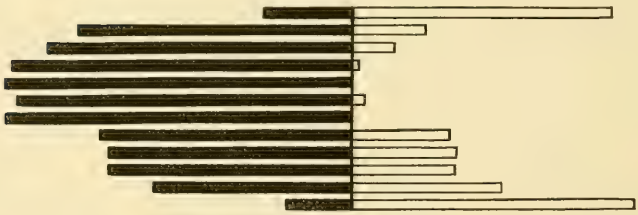


Fig. D.—Diagram showing change of food habits of the western meadowlark from month to month. Note that the maximum consumption of animal food is in April and May. Computed from stomach examinations of an average of six birds collected each month in a year at San Bernardino, San Bernardino County, California.

does change. This seems natural, for weather conditions affect the available food supply. Thus we find very few ants taken by meadowlarks collected at Newman, Stanislaus County, in 1911, but large numbers taken during the same months in 1912 (fig. E).

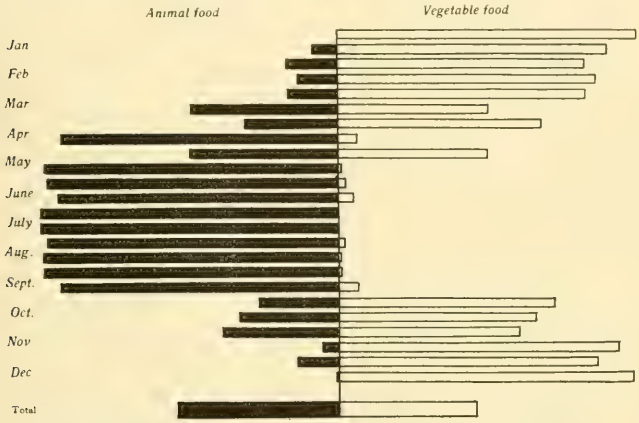


Fig. E.—Diagram showing the comparative amounts of the different kinds of food of the western meadowlark every two weeks during a year. Computed from the results of stomach examinations of birds collected at Newman, Stanislaus County, California.

The following table gives a comparison of the amounts of animal and vegetable food and the amounts of some of the common elements of food taken by meadowlarks at Newman, Stanislaus County, in 1911 and in 1912. The difference in amounts of animal and vegetable food is seven per cent. A large increase in 1912 of the number of grasshoppers taken can be noted. Seventy-two birds from each year were examined.

Comparison of Food of Meadowlark for Two Successive Years

Year	Per cent animal food	Per cent vegetable food	Per cent grain	Per cent grass-hoppers	Per cent beetles	Per cent ants
1911	53.5	46.5	38.4	27.5	8.5	.4
1912	65.7	34.3	32.3	42.4	9.9	3.0

Variation of Food Habits According to Locality

The comparison of the food of the western meadowlark in California has been made in several different ways. As soon as it was found definitely that the food varied greatly from one part of the state to the other, it was decided to make three groupings for comparison as follows: (1) districts; (2) counties; (3) localities. The wide difference in the kind and availability of food in the coast region and in the interior valleys makes this comparison of prime importance. Although a comparison by counties covers in a measure that by districts, yet this smaller unit of area brings to each rancher a knowledge of the food of the meadowlark in his own county. Although the difference in locality will parallel largely the difference in county, owing to the fact that usually but one series of birds was collected in each county, yet this comparison affords a knowledge as to the amount of variation between still smaller units of area.

Birds collected in the vicinity of San Diego took a smaller percentage of insects than those collected at Riverside and San Bernardino. Birds collected in the vicinity of Ukiah, Mendocino County, took larger numbers of click-beetles than birds from any other locality. Stomachs of birds collected in the vicinity of Hollister, San Benito County, contained extraordinarily large quantities of crickets. At Hanford, Kings County, birds fed very extensively on cutworms. Birds collected at Newman, Stanislaus County, contained extra large percentages of stink-bugs and grasshoppers. Birds from Red Bluff, Tehama County, Live Oak, Yuba County, Sacramento, Sacramento County, Newman, Stanislaus County, and Los Banos, Merced County, took very nearly the same proportion of animal and vegetable food.

Variation of Food According to Districts

For the purpose of comparison the following county groupings were made:

Humid Coast Belt:	Humboldt, Mendocino, Sonoma, Marin.
Interior Valleys:	Tehama, Sutter, Sacramento, San Joaquin, Alameda, Merced, Stanislaus, Madera, Fresno, Kern, Kings.
Mountain District:	Shasta, Lassen, Nevada, Calaveras.
Arid Coast Belt:	Ventura, Los Angeles, San Bernardino, Riverside, Orange, San Diego.
Desert:	Inyo, Imperial.

The following table gives the food of the western meadowlark in these districts:

TABLE SHOWING VARIATION OF FOOD ACCORDING TO DISTRICTS

	Number of birds	Per cent animal food	Per cent vegetable food
Humid Coast Belt	99	59.0	41.0
Interior valleys	785	61.8	38.2
Mountain district	27	69.6	30.4
Arid Coast Belt	536	58.5	41.5
Desert	58	63.0	37.0

By considering only those localities where complete or nearly complete series were obtained, a still more marked difference could be noted. If the results from an examination of more birds from the humid coast belt and mountain districts were available, the results would show a larger amount of animal food. The remarkable thing is that, considering the widely different climatic conditions, the food averages do not vary more than ten per cent.

INFLUENCE OF AGE AND SEX ON QUANTITY OF FOOD TAKEN

As the male weighs an ounce (28.35 grams) more than does the female, a difference of one-half cubic centimeter in capacity is accounted for. Juveniles average less food than adults. This is explainable on the ground that they are less experienced in obtaining food. Male and female nestlings apparently have more nearly the same capacity than do adults of different sexes.

A slight variation has been noted between the food of adults and young birds, both in kind and quantity. Young birds apparently lack the experience of the adults and pick up only the more conspicuous insects and weed seeds. They also lack the experience needed for catching certain insects, and therefore the stomachs average a little less in volume of food. It has been pointed out by Finn (1887) "that each bird has to separately acquire its experience, and it well remembers what it has learned." There appears to be little instinctive knowledge of the different kinds of food, and each young bird must test and learn. It would seem, therefore, that young birds would collect many so-called protected insects, whereas some experienced ones

would pass them by. This theory has not been supported by the results of this investigation, nor, on the other hand, has it been broken down. Although young birds were distinguished from adults, yet the unusual insects found were not constantly taken from the stomachs of young birds.

Combination of Field and Laboratory Work

Judd (1901) has suggested, as the best means of determining the food of birds, an examination of the available food supply combined with stomach examinations of birds taken in the same locality. There are many points which commend this method. Yet there is great difficulty in determining the available food supply. Even an experienced observer cannot estimate even with moderate accuracy the comparative numbers of insects and weed seeds in any given locality. A bird is able to see many articles of diet which such an observer doubtless overlooks. Let me cite a case in point: A meadowlark was seen to fly to a grain field and collect cutworms to feed its young. Careful investigation by me of the place where the cutworms were collected failed to reveal any. The same was noted with a pair of Brewer blackbirds who persistently collected cutworms in a pasture. Continued investigation in the same pasture did not allow of the collection of a single cutworm.

An attempt was made to follow this particular line of investigation, but was finally given up on account of the multitude of personal errors which are easily introduced. It seemed best to concentrate on the usual method of stomach examination, thereby making comparison with previous work possible.

Relation of Birds to Insect Outbreaks

The value of birds as insect destroyers is more noticeable at the time of an insect outbreak. Their importance in maintaining an equilibrium depends largely upon their effect when insects occur in abnormal numbers and thus become noticeably injurious. In two insect outbreaks investigated the western meadowlark was found to take a very active part in insect destruction.

During the spring and summer of 1911 the nymphalid butterfly *Eugonia californica* became very abundant in the northern part of the state. Since butterflies are seldom eaten by birds, the outbreak afforded a splendid opportunity to study the food habits of birds. Consequently an investigation was carried on during the latter part of August at Sisson, Siskiyou County, California, when these insects were in abnormal numbers.

Apparently because of the availability of the insect, several birds were found to be destroying butterflies. The Brewer blackbird (*Euphagus cyanocephalus*) fed on them almost exclusively, whereas the western meadowlark (*Sturnella neglecta*), western kingbird (*Tyrannus verticalis*), blue-fronted jay (*Cyanocitta stellari frontalis*), and Say phoebe (*Sayornis sayus*) took them sparingly. A comparison of the food of birds taken before the plague with that of birds taken while the plague was at its height showed that birds had varied their food habits and had taken advantage of the abundant supply of insect food in the form of butterflies.

Both observation and stomach examination showed the western meadowlark to feed on the butterfly (*Eugonia californica*). A lone meadowlark feeding with some Brewer blackbirds on the grass plot adjoining the station at Sisson was seen to run after several butterflies and to catch one. In the examination of seven stomachs, two contained butterflies. Fifteen and two-tenths per cent of the food taken by the five meadowlarks collected in August was made up of butterflies. All of these birds were taken in meadow or cut fields of wild hay where other insect life was abundant. Beetles and grasshoppers formed the bulk of the food.

Stronger evidence that birds turn their attention to the insect most available can hardly be found, for in this case we find a supposedly unpalatable insect becoming food for a number of species of birds. The United States Biological Survey, in the examination of more than 40,000 stomachs, has found but four records of birds eating butterflies, "and one of these probably relates to the capture of a very recently emerged specimen, or to one torn from the pupa before emergence, as it was accompanied by a pupa of the same species." (See McAtee, 1912c.)

Whether butterflies are too active to be caught, or whether they are unpalatable because of odor or taste, are questions still awaiting an answer. In any case it can truly be said that butterflies, considering their abundance, are not taken as food in anywhere near the proportion that other insects are taken. That four of the larger common birds of the region should have fed upon these insects and that one of these should have fed almost entirely upon them is certainly significant.

It cannot be said that lack of other food caused these birds to turn their attention to butterflies, for many of the birds collected had either taken no butterflies or but one or two. The butterflies were not only conspicuous, but extremely abundant. Some idea of their numbers can be obtained when it is known that in damp places or along the banks of streams, where the butterflies had gathered to drink, as many as one hundred and fifty individuals were counted in one square foot. In order to estimate the numbers flying counts were made of the individuals passing between two fir trees about twenty feet high and standing about thirty feet apart. The counts for ten successive minutes between 4:40 and 4:50 P.M. on August 20, 1911, were as follows:

1st minute	105	7th minute	96
2nd minute	119	8th minute	102
3rd minute	130	9th minute	83
4th minute	102	10th minute	112
5th minute	134		
6th minute	100	Av. per minute	108

It can readily be seen, therefore, that butterflies were the insects most available at the time. The significant thing is that certain birds changed their food habits to meet the changed conditions. Birds collected in the same locality before the butterflies became abundant had taken no butterflies.

The investigation did not show that birds can be depended upon to control butterfly outbreaks, for the numbers taken compared with the actual numbers of the insects were insignificant. The fact that the birds attacked the insect at a critical time in its life-history—the adult stage when the death rate is at its minimum and the insect has the best chance of surviving till egg-laying—made the work of birds more important than if they

had fed upon the larvae or pupae. However, any increased destruction at the time when insects appear in abnormal numbers must be considered a benefit.

Four out of the five birds found to feed on the butterflies are numbered among the birds whose usual food habits justly subject them to severe criticism from the farmer. Consequently the conclusion can be drawn that some of the birds noted for their depredations often become valuable insect destroyers at just the time when they are most needed as such.

This evidence fails to support Mr. McAtee's contention that "butterflies are in very little demand with birds in the United States." Nor, on the other hand, does it support the conclusions of Finn (1897) that "there is a general appetite for butterflies among insectivorous birds, even though they are rarely seen when wild to attack them." Middle ground seems to be the best position to assume until more evidence is at hand.

In our attempt to explain why butterflies are seldom taken by birds we have laid emphasis on palatability. This factor can at best be but one of many factors, many of which are perhaps just as important if not more important. Then, too, it should be noted that palatability is an extremely variable factor, for it varies with the species, the time of year, the availability of food, etc. We still need a full examination of all of the factors governing the food-taking of birds in order to explain the interrelation between birds and butterflies.

In an investigation of a grasshopper outbreak at Los Banos, Merced County, in July, 1912, it was found that western meadowlarks were destroying an average of nearly fifty grasshoppers a day. From point of numbers and average number of grasshoppers destroyed, the western meadowlark was, next to the bicolored red-wing, the most efficient destroyer of the pests. Meadowlarks averaged more grasshoppers per bird and were outdone by the red-wings only when the numbers of individual birds and the total destruction accomplished by each species were considered.

A comparison of the food of meadowlarks taken in the same locality in 1911, when grasshoppers were not so abundant as they were in 1912, demonstrated the fact that meadowlarks averaged more grasshoppers when these insects were abnormally abundant

than they did when they were not so abundant. The results of stomach examinations follow:

Food of Western Meadowlark at Los Banos, Merced County, California

Number of birds	Date	Animal food	Vegetable food	Average no. of grass-hoppers per bird	Total per cent grass-hoppers
10	July 11, 22, 1911	99.0	1.0	7	83.1
5	July 15, 17, 1912	99.2	.8	16	96.2

Meadowlarks took very nearly the same percentage (99, 99.2 per cent) of animal food each year at the same season, showing that at this time of year the bird is almost wholly insectivorous. The availability of grasshoppers as a diet appears to have influenced the birds taken in 1912, for they averaged sixteen grasshoppers apiece as against seven taken by birds collected in 1911.

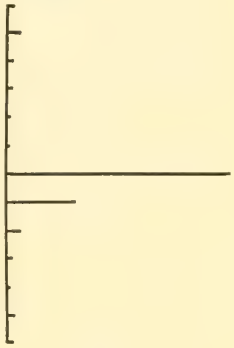
As the numbers of grasshoppers in 1911, compared with the numbers in 1912, is not definitely known, it is impossible to state whether these birds changed their food habits in response to the extreme availability of the insects in 1912. It is also impossible to state whether the numbers taken in 1912 were in direct proportion to the numbers taken in 1911 or whether they failed fully to respond to the change in insect population. The fact remains, however, that meadowlarks, and other birds as well, took greater numbers of grasshoppers when they were abnormally abundant, but also forsook certain articles of diet, such as beetles and weed seeds, thus causing an increased percentage of grasshoppers to be taken as food. The direction of the change of food habits was certainly coincident with the direction of change in food supply.

The efficiency of a bird as an insect destroyer at the time of an insect outbreak is governed more largely by the numbers of birds than by their individual capacity. This was conclusively shown in the investigation of the grasshopper outbreak. The comparative destruction of grasshoppers per day by single individuals and by the total number of each species is represented in the following table:

Comparative Daily Destruction of Grasshoppers by Birds

Species	Class	Average no. of grasshoppers per day by One bird	Average no. of grasshoppers per day by Total population
Anthony Green Heron	B	42	1,050
Killdeer	B	33	5,445
Burrowing Owl	A	84	1,260
Western Kingbird	D	8	1,280
Black Phoebe	D	9	180
California Horned Lark	D	8	88
Bicolored Red-wing	B	29	78,590
Western Meadowlark	B	48	24,720
Bullock Oriole	B	45	4,050
Brewer Blackbird	D	9	225
English Sparrow	D	2	100
Cliff Swallow	D	3	2,265
California Shrike	C	12	1,200
Destruction per square mile by total bird population			120,453

Relative destruction by different species represented by lines



Class A represents birds taking an average of over 50 grasshoppers per day; class B, 25–50; class C, 10–25; and class D, fewer than 10 grasshoppers.

The comparative numbers of the different species were calculated by averaging censuses taken and by using the average per mile as a multiplier. Although not accurate, the table nevertheless demonstrates the fact that such birds as the bicolored red-wing and the western meadowlark, birds of small capacity, because of their greater numbers, far outrank in efficiency birds with larger individual capacity.

The fact that the western meadowlark, or any bird, turns its attention to the insect most abundant only emphasizes its value as a balancer. If meadowlarks took no greater proportion of insects when they are in abnormal numbers than when they were in normal numbers, they would play a decreasing part in restoring a balance. Since they do change the proportions of food to meet the fluctuations in the number of insects, they must be considered an important factor in the restoration of normal conditions.

A great number of factors operating together determine the abundance of an insect. Birds and other natural enemies are but one of these many factors. The rate of reproduction and food supply are probably more important factors. In spite of this fact birds are one of the limiting factors and are deserving of attention as such.

The following facts have been demonstrated by these investigations:

1. Birds cannot be considered a dependable means of completely controlling all insect outbreaks, but can be inferred to be instrumental in the prevention of many.

2. Birds can be depended upon to act as defenders and protectors of crops because of their warfare against insect pests.

3. Birds change their food habits and feed on the insect most abundant, thereby making themselves important maintainers of the desired balance in nature.

4. The failure of birds to check an insect outbreak entirely is evident to all. Their success in preventing insects from becoming abundant is not so apparent, but is none the less real. All obtainable evidence points to the fact that the regulative influence exerted by birds when insects are to be found in normal numbers, though less apparent, is none the less important, for at such times artificial control measures are seldom used.

5. Birds, which on account of their abundance cause serious losses to the agriculturist, often become for the same reason the most efficient insect destroyers at the time of an insect outbreak.

6. Birds help to maintain an equilibrium in nature. Their destruction, therefore, causes a dangerous disturbance of that balance of nature most suited to mankind.

Verdict of Ranchers

In order that the opinion of the men most directly concerned might not be overlooked, a circular letter was sent out to prominent ranchers throughout the state. A copy of the letter follows:

Dear Sir:—

The State Fish and Game Commission has taken up the study of the meadowlark in its relation to agriculture and desires to know what you think of the bird. In order to secure comprehensive and uniform data, answers to the following questions are urgently requested:

1. Name .....
2. Address .....
3. Occupation .....
4. How many acres of land do you own? .....
   Is your ranch hilly upland or bottom land? .....
5. What is the principal crop raised? .....
   What other crops? .....
6. Has the meadowlark done any harm on your place? .....
   If so, how and to what extent? .....
7. Have you examined the stomachs of any meadowlarks to ascertain their food? ..... If so, what was in the stomachs? .....
8. Approximately, how many meadowlarks are seen daily on your place? ..... Are the numbers any greater when the grain is sprouting? .....
9. Do you prize the meadowlark as a song bird? .....
10. On the whole, do you consider the meadowlark a nuisance? .....

Any additional information that you can give on the subject will be appreciated. Address all communications to H. C. Bryant, Assistant State Fish and Game Commission, East Hall, University of California, Berkeley, California.

Over a hundred replies to this letter were received. Although the returns may be criticised on the grounds that a greater number of those interested in the bird because of its esthetic value sent in answers, yet care was taken to avoid this. Blanks were sent to the men who complained of the depredations of the meadowlark and to ranchers irrespective of their particular point of view. The average acreage of the men reporting was 638, so that it can be seen that the verdict is not from small land-holders or orchardists. Over ninety-eight per cent of those reporting grew grain or hay.

When the returns as to whether the meadowlark is a nuisance and as to whether it damages crops are classified as to counties the results are as follows:

County	Number reporting	Is the meadowlark a nuisance?		Does the meadowlark damage crops?	
		Yes	No	Yes	No
Siskiyou	5	.....	5	.....	5
Shasta	1	.....	1	.....	1
Humboldt	2	.....	2	.....	2
Trinity	5	1?	4	.....	5
Mendocino	1	1	.....	1	.....
Tehama	3	2	1	2	1
Sutter	5	5	.....	5	.....

County	Number reporting	Is the meadowlark a nuisance?		Does the meadowlark damage crops?	
		Yes	No	Yes	No
Plumas	1	.....	1	.....	1
Butte	2	2	.....	2	.....
Yolo	1	1	.....	1	.....
Sonoma	4	4	.....	4	.....
Napa	2	1	1	1	1
Sacramento	2	1	1	1	1
Marin	1	.....	1	1	.....
Contra Costa	1	.....	1	.....	1
Alameda	7	2	4	3	4
San Joaquin	17	11	5	11	6
Stanislaus	2	.....	2	.....	2
El Dorado	1	1	.....	1	.....
Calaveras	1	1	.....	1	.....
Madera	1	1	.....	1	.....
Merced	3	.....	2	1	2
Fresno	5	4	1	4	1
Monterey	9	2	7	2	6
San Luis Obispo	1	1	.....	1	.....
Kings	5	3	1	4	1
Tulare	4	1	.....	3	1
Mono	3	.....	3	.....	3
Inyo	9	2	7	2	7
Kern	1	.....	.....	.....	1
Santa Barbara	3	.....	3	.....	3
Ventura	.....	.....	.....	.....	.....
Los Angeles	2	.....	2	.....	2
San Bernardino	1	.....	1	.....	1
Orange	5	.....	4	.....	5
Riverside	4	1	3	2	2
San Diego	2	.....	2	.....	2
Imperial	.....	.....	.....	.....	.....
Totals	122	48	65	54	67
Total coast counties	31	5	25	5	25
Total central counties	60	35	19	38	22
Total northern California	105	47	50	52	52
Total southern California	17	1	15	2	15

It will be seen from this table that there is a considerable difference of opinion as to whether the western meadowlark damages crops. The astonishing fact is that many grain growers in the Sacramento and San Joaquin valleys report that western meadowlarks do not injure their crops, or that the injury is negligible.

The kinds of crops reported as being damaged ranged from garden truck, melons and grapes to corn and sprouting grain. Damage to garden truck, melons and grapes was reported by three or fewer men. Damage to oats was reported by over twenty, barley by less than this number, and wheat by less than ten. Most of the reports did not designate the kind of grain, simply stating that meadowlarks damaged sprouting grain. Answers as to the extent of damage varied from "none" to "total crop." The number of meadowlarks seen was reported as being from two or three up into the thousands. The answers to this question cannot be considered reliable. A large majority of those who considered the meadowlark a nuisance answered the question whether the meadowlark was prized as a song bird in the negative, whereas those answering the former question in the negative almost unanimously answered the latter in the affirmative.

Reports of damage were most numerous from the Sacramento and San Joaquin valleys. This seems natural, for grain is the crop most widely grown in this section and meadowlarks are most numerous. Southern California is most unanimous in its verdict of "not guilty." Two reasons can be made to account for this: the comparatively small amount of grain raised and the comparatively small number of meadowlarks. Few reports of damage have come from the northern coast region, in spite of the fact that meadowlarks are very numerous in this section.

The majority of those reporting have not had crops damaged by meadowlarks and do not consider the bird a nuisance. It does not seem reasonable to believe that all of these men based their report on sentiment. Evidence seems to point rather to the fact that many of those complaining of damage have based their judgment on circumstantial evidence and have somewhat exaggerated the real damage done.

A Determination of the Economic Status of the Western Meadowlark in California

Field investigation of the damage to crops has led to the following conclusions:

1. The western meadowlark is destructive to sprouting grain because of its habit of boring down beside the sprout and pulling off the kernel. The amount of damage varies with the location, the abundance of the birds, the time of year, the character of the soil, and the kind of grain. The damage to oats is greatest; wheat suffers less and barley little. A greater loss can be expected with broadcasted grain than with drilled grain, because not being sowed so deeply it is more readily obtained by meadowlarks. The real amount of damage done has evidently been overestimated, however, for fields apparently badly damaged have given the average yield later in the year. On the other hand, where meadowlarks are very numerous and the quantity of grain small, fields have had to be resown to assure a crop.

2. In the destruction of sprouting grain we have the only serious count against the meadowlark, for damage to melons, grapes and other crops has been found to be negligible. A number of things minimize the damage done, chief of which is the fact that meadowlarks are able to obtain the kernel for a limited period only. After the second and third leaves have appeared, the plant is well rooted and the loss of the kernel does not destroy the plant. Hence damage is limited to a period of about two weeks on any given field and is reduced by deep planting.

3. Those factors which make the depredations of the western meadowlark important and those factors which minimize the damage done may be summarized as follows:

1. Method of pulling sprouting grain.	1. Same method valuable in securing such insects as cutworms and wireworms.
2. Lack of insect food when grain is sprouting coupled with the availability of grain at the same time.	2. Take a larger percentage of insects than of grain during year.
3. Flocking habit.	3. Apparently driven to grain only when insects are not available.

4. Abundance of meadowlarks in grain-growing localities.
5. Great capacity and rapid digestion.

4. Time during which damage can result limited.
5. Flocking habit makes control measures easier.
6. Abundance of meadowlarks assures more efficient destruction of insect pests.
7. Great capacity and rapid digestion improves their value as insect destroyers; slower digestion of grain than of insects makes a less consumption of the former.
8. Do not destroy other crops.
9. A certain amount of thinning is sometimes desirable.
10. Often perform service in destroying insects in same field where damage was done.
11. Prefer uncultivated to cultivated land.
12. Unable to cause serious damage when grain is planted deeply.

4. A study of the life-history of the western meadowlark shows it to be a bird which prefers uncultivated to cultivated land, especially while feeding and nesting. It feeds in places where other birds do not feed, and takes many of the ground-loving insects which other birds do not take. Its habit of boring into the ground after food makes it important as a destroyer of such insects as cutworms, wireworms, and tipulid larvae, very destructive insects of the grain fields and meadows. Young birds are fed entirely on insects and need nearly their own weight of food each day. They demand the largest amount of food when insects are at a maximum. The western meadowlark appears to increase in numbers with cultivation of land when a proper food supply is furnished. It can be seen, therefore, that most of the facts regarding its life-history tend to place it among the beneficial birds.

5. Experimentation has shown that western meadowlarks, like other birds, have a very rapid digestion and are able to digest a full meal in four to six hours. Under these circumstances it is evident that they must consume large quantities of food. Ex-

perimental feeding has substantiated this fact. The larger the amount of food consumed the larger must be the toll taken. As experiment showed that insects are digested more rapidly than grain, proportionately larger amounts of insect food than vegetable food may be consumed daily.

6. Stomach examination has demonstrated the following facts: (1) A much larger percentage of animal food (sixty per cent) is taken during the year than vegetable food (forty per cent). The meadowlark feeds on grain to a considerable extent during the winter months. A very small proportion of that found in the stomachs was sprouted grain. A large proportion of the grain taken was made up of wild oats and had evidently not been gathered in grain fields. If meadowlarks by their depredations can drive many of the ranchers of the state to drill their grain and plant it more deeply they will be performing a service by increasing the yield. The increased yield so produced would doubtless more than cover the loss sustained from the birds.

(2) Western meadowlarks destroy large numbers of insects which are injurious to the same crop damaged by the birds themselves.

(3) The kind of food varies with time of year, locality, and abundance of available food. This correlation of food habits with the environmental conditions increases the bird's value as a balancer. If the meadowlark did not change its food with a change in supply, its value as an insect destroyer would be slight. In turning its attention to the food most abundant it becomes an important factor in maintaining a balance. Its survival as a destroyer of insects is dependent on its being able to obtain a supply of food when animal food is not available.

(4) The quantity of injurious insects taken daily is large enough to make this bird of at least some importance as a destroyer of insect pests. The cumulative effect of such destruction enhances the bird's value. Few beneficial insects are destroyed.

(5) The meadowlark destroys quantities of seeds of serious weed pests.

The service which birds render to agriculture has been overemphasized by those appreciating the esthetic value of birds.

Such writers have been prone to take the point of view that birds were expressly made to destroy injurious insects. One might just as well say that insects were created to furnish food for birds. If birds should become numerous enough actually to control the number of insects, they would doubtless become a greater pest than the insects themselves.

Parasitic insects are not proving to be the controls which their advocates have maintained they would be. And certainly there are arguments which prove that birds are not the panacea for all insect ills. Birds destroy many of the most beneficial insects known. Some of the most injurious insects are less often taken by birds. Birds, though they be in abundance, fail to prevent outbreaks of injurious insects. Birds scatter weed seed as well as destroy it. If there were no birds, would not other factors, such as parasitism, climatic conditions, etc., soon bring about a balance? Besides, cannot insect pests be more surely and successfully controlled by artificial means, insecticides, sprays, etc.? On the other hand, is there not a saving of expense in letting nature control insect ravages as far as possible?

All of these points deserve our consideration. They need to be weighed in the balance. When all the evidence for and against the utility of birds is in, a solution will be available. Until that time there will always be two sides to the question.

A partial solution of the problem is afforded by placing emphasis elsewhere, thereby avoiding these two opposing sides of the question. Forbes (1903) pointed out that the value of birds does not lie in the fact that they discriminate and take only injurious insects, but in the fact that they eat insects. The place filled by birds in the economy of nature is the important thing.

Most life under the natural order of things is conditioned very largely by its food supply: in the case of purely insectivorous birds, by insects; in the case of insects, by plant life. If it be true, as it appears to be, that organisms become so adjusted to their food supplies that only the surplus or excess is normally taken, then the importance of birds in their relation with insects lies in their toll of the surplus. Since it is the excess or abnormal abundance of insects that makes most trouble for the agricul-

turist and horticulturist, any factor, even though it be one of many factors, is important in insect control. Birds destroy insects; they are therefore a natural factor in the control of insect life. Since they do not fluctuate in numbers so greatly as do parasitic insects, they are a more constant factor than parasites. Insectivorous birds feed on the insect most abundant, hence they are the more important in limiting the numbers of insects. The proportion taken apparently varies directly as the numbers of the insects. The greatest toll on insect life comes during the nesting season, a time when the insect population is at its maximum. This in itself establishes the fact that birds have a real and an important part to play in the interaction of organisms.

Almost all insects are potentially injurious. Injurious insects in small numbers cause practically no damage. Neutral and beneficial insects in large numbers may become injurious. Hence the destruction of neutral and beneficial insects, if they are potentially destructive, may become at times of utility.

Insects have in turn adapted themselves to the constant drain on their numbers. This becomes very evident when we study the rate of reproduction of insects. However, it is the balance we need. Birds and insects both have a part to play in the balance. They are supplementary and indispensable.

This is an important viewpoint. Emphasis on the relation of birds to insects viewed from the standpoint of the interaction of organisms is rightly placed. Birds are important because they evidently are an indispensable factor in maintaining an equilibrium of organic life. If all birds play this important part, the destruction of any particular species of bird means a disturbance in the balance. The nearer man adjusts organic life to his desires the more important will become each natural factor concerned. Artificial means of adjustment often lack the efficiency of natural means.

It is readily acknowledged that birds are not the only checks on the increase of insects. The very large toll taken by them, however, places them in the front rank as insect destroyers. Parasites can become abundant only when their host becomes abundant and do their work effectively only after the insect has

had sufficient time to cause damage. Birds in order to keep alive must wage a continual warfare on insect life, no matter what the abundance. They are evidently, therefore, to be relied upon as more dependable regulators than parasites.

Since, as has been shown, the average adult western meadowlark destroys nearly three pounds of insects each year and probably almost as many more pounds while feeding its young, its value to the agriculturist is apparent. The ratio of value of one of these birds living to that of one dead is, therefore, as five pounds of insects and one-half pound of weed seeds are to one and three-fourths pounds of grain, a considerable portion of which is made up of wild oats and waste grain.

The fact that the western meadowlark destroys certain beneficial insects cannot be counted a point in its favor. And yet the quantity taken is so small, less than five per cent of the food for the year, and the destruction so caused is such an indirect injury, that the damage possible is very slight and practically negligible. The destruction of one ichneumon-fly compared with the destruction of one hundred grasshoppers, somewhat the proportion in which they are taken, leaves no doubt as to the comparative benefit.

Since the western meadowlark feeds to a large extent on grass-land insects, many of which are not eaten by other birds, it must be considered a friend of the dairymen and grain growers, and not an enemy. "The laborer is worthy of his hire." The grain taken by western meadowlarks can well be considered the pay for their efficient work in destroying injurious insects and weed seed.

It must be apparent from these comparisons that the balance is certainly in favor of the meadowlark. Birds are considered a national resource and so belong to the people as a whole. It seems doubtful whether the grain grower should destroy birds destroying his crops when the same birds might be performing a great service in destroying injurious insects in his own or his neighbor's alfalfa field.

This investigation has shown that the western meadowlark, as a rule, deserves protection and encouragement at the hands of the agriculturist. Only in rare cases can it be said that the

bird does more harm than good. One and three-fourths quarts of insects taken by a western meadowlark during a year more than pay for less than one quart of grain, a large part of which does not represent a loss.

Although emphasis has been laid on the dollar and cents value, yet the other values which cannot be reckoned on the money basis must be taken into account. And here we find an even stronger defense of the western meadowlark, for the esthetic and scientific values greatly strengthen the case for the bird, in spite of the fact that these values are often unacknowledged by many who profit by them.

The investigation has shown that for the following ten reasons the western meadowlark should remain a protected non-game bird.

TEN REASONS WHY THE WESTERN MEADOWLARK (*STURNELLA NEGLECTA*) SHOULD BE A PROTECTED NON-GAME BIRD

1. As a destroyer of cutworms, caterpillars, and grasshoppers, three of the worst insect pests in the State of California, the western meadowlark is probably unequaled by any other bird. The stomachs of meadowlarks examined have averaged as high as six cutworms and caterpillars, and sixteen grasshoppers apiece. Maximum numbers of sixty-six cutworms and of thirty-two grasshoppers have been taken from a single stomach. As the time of digestion is about four hours, three times the average must be consumed daily. Other injurious insects destroyed are click-beetles, the larvae of which are wireworms, May beetles, weevils, crickets, Jerusalem crickets, stink-bugs, flies, and crane-flies. Fifty-nine and six-tenths per cent of the food for the year is made up of animal food. Each meadowlark in the state consumes, at the least calculation, six pounds of food each year, two and three-fourths pounds of which is made up of insects, most of which are injurious to crops.

2. The western meadowlark destroys a very small percentage of beneficial insects. That one hundred grasshoppers are destroyed to every parasitic ichneumon-fly is a very conservative estimate.

3. But one crop is attacked, for the only serious loss occasioned by the western meadowlark is to sprouting grain. Damage to fields of sprouting grain can be largely prevented by certain protective measures, some of which have been proved by experiment to be instrumental in producing better crops. Hence injury to crops is not only limited but largely preventable.

4. The western meadowlark destroys the seeds of some of California's worst weed-seed pests. During the fall months, when insects are not available, this bird destroys large quanties of weed seeds. Over two hundred weed seeds have been taken from a single stomach. Napa thistle, Johnson grass, canary grass, foxtail, tarweed, pigweed, tumbleweed, mustard, turkey mullein, sunflower, and nightshade are among the weed pests destroyed.

5. The western meadowlark, by feeding in places not frequented by other birds, procures many injurious insects which would not fall prey to other animals. In so doing it fills a niche in the economy of nature which apparently is not filled by any other form of life.

6. Investigations of the relations of birds to insect outbreaks have demonstrated that the western meadowlark, by turning its attention to the insect most available, becomes important as a maintainer of a balance of insect life. As such it becomes a defender and protector of crops.

7. The western meadowlark has great esthetic value. A bird of the meadow and pasture, it adds life and interest to treeless areas. Its bright colors and beautiful song have made it one of the best known birds in the state. The meadowlark even adds to the value of suburban real estate.

8. The western meadowlark cannot be considered a game bird. The following quotation is from an article by D. G. Elliott (1864), entitled "The Game Birds of the United States": "Not indeed every feathered biped, which a high breed of dogs will instinctively point, can be included in our list; for the meadowlark (*Sturnella magna*), that troublesome pest of every true

sportsman, whose dog, unless taught otherwise, will surely follow, has fairly no claim to this title, any more than have a snake or a turtle, to either of which a point will generally be made, and these last, it is hardly necessary to add, are neither birds nor game.'' In some of the eastern states, where the meadowlark is still unprotected, a parasitic worm often found in the small of the back deters many experienced persons from using the bird for food. The western meadowlark cannot be considered a game bird under the definition of such birds given in Section 637a of the Penal Code of the State of California.

9. By a decision of the United States Supreme Court (Geer v. Conn., 161 U. S. 519), birds are considered a national resource belonging to the people as a whole. The destruction of the western meadowlark by the grain grower causes a loss to the growers of alfalfa and other crops who profit enormously by the destruction of insect pests by the bird.

10. In certain sections of California, notably southern California, because of the small numbers of meadowlarks or owing to the kind of crops raised, the western meadowlark causes no damage and is considered distinctly beneficial. The extent of damage varies with the locality and the kind of crop raised.

Suggestions for the Protection of Crops

In a study of this kind something should be said as to the methods of protecting crops from the depredations of the western meadowlark, for, although we may in general say that the bird is highly beneficial to agricultural interests, yet local conditions and an overabundance of birds may demand protective measures. Scarecrows have proved inefficient as a means of protecting grain fields from attack by meadowlarks. The birds soon become accustomed to any object placed in the field, and so continue their depredations. Frightening the birds by shooting is found to be a better means, but is not always practical. It should be remembered that the protective measures suggested are all practical ones, for it has been shown that the damage is limited to two weeks; also that a certain amount of thinning is allowable, and in some cases of value. The outlay of several extra sacks

of grain can be more than counter-balanced by the efficiency of the meadowlarks later in the year when injurious insects have become abundant in grain fields.

Where losses to crops warrant protective measures the following are proposed:

1. Plant grain deeply. It assures a better crop regardless of losses due to meadowlarks. Drilled grain gives a better yield than broadcasted and is also better protected from the attack of meadowlarks.

2. Fields bordering pasture or uncultivated land, if sowed more heavily along such margins, will usually be assured a normal crop.

3. Meadowlarks are easily frightened from a field by the noise of shooting or by a dog. As damage is limited to a short period of time, this method seems practical on small fields.

Recommendations as to Legislation

The United States Supreme Court (Geer v. Conn., 161 U. S. 519) has ruled that all game and wild birds belong to the people. The decision of the court in a test case in California is as follows: "We take it to be the correct doctrine in this country that the ownership of wild animals, so far as they are capable of ownership, is in the State, not as a proprietor, but in its sovereign capacity as the representative and for the benefit of all its people in common (State v. Rodman, *l. c.*). Consequently the people, through their various legislatures, control this natural resource. It is evident, therefore, that as in other things, the majority rule. In legislation the rights of the many are often clouded over by the activities of the few. Sometimes this is due to inactivity on the part of the many; sometimes it is due to a lack of knowledge on the part of the many and an accurate knowledge by the few. In the case before us we desire that there shall be no lack of information on either side.

The desire on the part of certain ranchers of the state to place the western meadowlark on the unprotected list in the hope that it might be so reduced in numbers as to prevent injury to crops, and the desire of certain sportsmen to add this bird

to the list of game birds, has twice occasioned the introduction of a bill into the State Legislature. The same influences caused the Fish and Game Protective Association in 1912 to recommend placing this bird on the game list. In spite of the failure of the former bills to pass, protest has continued. As a final solution of the problem this investigation was ordered by the State Fish and Game Commission.

* * * * * * * * * * *

This investigation having been completed and dependable data being at hand, the following considerations appear to the writer to demand the accompanying recommendation for legislation:

The western meadowlark (*Sturnella neglecta*), along with other birds, must be considered an important resource of this state, and therefore cannot receive destruction at the hands of some without distinct loss to others.

The western meadowlark can in no way be considered a desirable game bird, but must be numbered with the insectivorous non-game birds.

The western meadowlark, through a thorough scientific investigation lasting over a period of over two years and including field study and an examination of nearly two thousand stomachs, some being collected each month of the year in over twenty different localities in California, has been shown to be distinctly beneficial to agricultural interests as a whole and thus to all the people of the state.

The western meadowlark has an esthetic value greater than that of almost any other bird in the state. This value, although not capable of expression in dollars and cents, is nevertheless real.

Sufficient protection from the depredations of the western meadowlark is afforded the farmers of the state through a law providing for the "killing of a meadowlark, robin, or other wild bird by the owner or tenant of any premises, where such bird is found destroying berries, fruit or crops growing on such premises."

For these reasons, *the western meadowlark (Sturnella neglecta) should be retained on the list of protected non-game birds of the State of California and should at all times be afforded the protection it merits.*

SOME INTERESTING SIDE-LIGHTS ON THE INVESTIGATION

In an investigation of this kind where so many birds of the same species have come to hand it would be unfortunate if some account were not taken of certain scientific problems such as variation, parasitism, etc.

Parasitism

Owing to the fact that birds were received in the laboratory preserved in formalin it has been impossible to examine them for blood parasites. The only parasites discovered have been nematodes (*Spiroptera* sp. ?), which have been found in the body cavity and more often in the intestine. Fewer than one one-hundredth of one per cent of the birds examined, however, were found to be infected. Hence western meadowlarks do not appear to be parasitized to any great extent by round worms. Western robins have shown a larger percentage of infection.

T. G. Pearson (1909) says of the eastern meadowlark: "A parasitic worm often found in the small of the back deters many experienced persons, however, from pursuing the bird persistently." Whether the western meadowlark is parasitized to a greater or less extent is not known, owing to the lack of data on the eastern meadowlark in this regard.

Tachinid larvae have been taken from the stomachs of meadowlarks. As these larvae are common parasites of grasshoppers and crickets, their presence in the stomachs would seem to be easily explained. However, in two cases at least they were eaten separately, for no grasshoppers or crickets were found in the stomachs containing the larvae.

Malformation

Three or four birds received in the laboratory had lost a foot or leg. In each instance the end of the broken tarsus had become enlarged and hardened by use. One bird, handicapped by the loss of both tarsi, was dwarfed.

Albinism

No cases of albinism in the meadowlarks received in the laboratory have been noted. Variations in the amounts of black, yellow, and white markings have been noted, however. Specimens received from the northern coast region have been the darkest in color, those from the southeastern arid regions the lightest in color.

Abundance of the Different Sexes and of Juveniles

If the numbers of the sexes collected is any criterion of their comparative numbers, it must be conceded that males are more abundant. Fifty-eight per cent of one thousand birds received from ten different localities were males. Collectors usually obtained a larger percentage of males the first few months. This can be explained on the grounds that the male is a larger and more conspicuous bird. Then, too, it is the bird most often seen during the nesting season.

About seventy per cent of the birds collected during the summer months were juveniles. This must correspond, to some extent at least, with the comparative numbers in the field.

Incubation and Moult

If judged by the condition of the feathers on the breast, females do most of the incubation. Breeding males were noted as early as late February and as late as August.

None of the birds has been largely denuded of feathers even during the moulting period. At no time do they appear to be greatly hindered by moult.

Effect of Systematic Destruction on Numbers

A systematic destruction of birds having been carried on in connection with this investigation, there appeared an opportunity to obtain evidence as to the result which might be expected as regards a decrease in numbers. Consequently a letter was written to deputies enquiring whether there had been a perceptible decrease in the numbers of birds in the localities where collections

were made. In every instance where a reply was received the deputy reported no noticeable decrease in numbers. As over two hundred western meadowlarks were collected during the year in several localities it would seem that a decrease might be in evidence. Of course, where meadowlarks are abundant such decrease would be hard to detect. However, in southern California, where meadowlarks are not so abundant, it seems strange that a decrease was not apparent.

This evidence lends support to the view that the meadowlark is a hardy, prolific bird and is capable of withstanding depletion far better than certain other birds. What the effect of placing the bird on the game list would be is not difficult to conjecture. The continued, systematic destruction which such a move would make possible would certainly have a greater effect on numbers than this comparatively slight destruction limited to not more than two years.

Death Rate

That there is a comparatively small percentage of young birds which grow to maturity is supported by the fact that during a two weeks' stay in a region where western meadowlarks were nesting abundantly, three dead nestlings were found at different times and in addition a nest of four destroyed by a hawk or weasel. The rearing of two broods, averaging three each, also supports this view. The death rate, if computed from the average number of young hatched, would be seventy-five per cent, for only two (twenty-five per cent) out of every eight survive if the population remains the same. The minimum number of meadowlarks can be expected just before the breeding season. As the minimum number remains fairly constant from year to year, it can be seen that from every pair of breeding meadowlarks, if they lived but one year, it would be possible for an average maximum of only two to reach maturity. Since the adults must live a number of years the death rate must be greater than seventy-five per cent.

The two greatest factors in the death rate are available food supply and natural enemies.

Do Protective Adaptations of Insects Protect Them From the Attacks of Birds?

In the attempt to interpret the law of natural selection emphasis has been laid on the "importance of any structure or character which enables its possessor to escape destruction." As soon as we find that one animal preys on another, we immediately seek for some character to which we can ascribe the survival of the hunted form. This has led to an overemphasis on the theory of protective adaptations.

Doubtless the interpretation we have put upon certain color characters and other characters called protective have been of value, just as our imperfect systems of classification have been of value. Yet, just as we are constantly changing and modifying original classifications, so we may expect to modify our views concerning protective adaptations.

In order to point out the view usually held, attention is called to the following quotation from Kellogg (1908): "It has been conclusively shown by observation and experiment, by several naturalists, that many insects are distasteful to birds, lizards and other enemies of the insect class. The blood, lymph or some specially secreted body fluid of these insects contains an acrid or ill-tasting substance, so that birds will not, if they can recognize the kind of insect, make any attempt to catch or eat them."

Kellogg also goes on to suggest the theory that "success" is dependent on protective adaptations. Certain animals are widespread and found in great numbers and certain others in small numbers. Those existing in great numbers are said to do so because they are protected from their enemies. Enemies are only one factor in the complex that governs the abundance or scarcity of a species, so that such a theory hardly seems justified.

The examination of so large a number of stomachs of one species of bird has furnished some interesting evidence regarding the extent to which certain insects are protected from their enemies. The evidence shows that many of the so-called protective adaptations of insects do not protect them from the attacks of enemies to the extent to which we have been led to believe.

A recent paper by W. L. McAtee (1912d) of the U. S. Biological Survey, entitled "The experimental method of testing the

efficiency of warning and cryptic coloration in protecting animals from their enemies," clearly points out the fact that the tests of protective adaptations against natural enemies have been inconsistent, misinterpreted, and are untrustworthy guides to behavior under natural conditions.

Investigators using the experimental method have too often failed to take into account other factors instrumental in modifying the behavior of animals toward their prey. "The rejection of various items of food by captive animals does not prove that these items are rejected by the same species under natural conditions." It does give some idea of the food habits, but does not furnish dependable evidence as to the food of birds in the wild.

More reliance can be placed on the evidence furnished by stomach examination, for "there is no possibility of going back of such evidence on the choice of food." Its one drawback is that it does not furnish us with data as to what was not chosen.

Hence the following evidence must be considered as valuable in throwing light upon this much discussed problem. The discussion will be largely directed to such protective adaptations as stings, noxious secretions, hairs, etc., as the evidence at hand bears more directly on this phase of the subject.

More has been written on the palatability of butterflies than on any other insect. To back up the theory of mimicry it was necessary that birds be made an important enemy of butterflies. That birds are an important enemy of butterflies still remains to be proved. The fact that the records of the United States Biological Survey show that in the examination of 40,000 stomachs of birds but four cases have been found where the birds concerned had eaten butterflies would support Mr. McAtee's contention that "butterflies are in very little demand with birds in the United States." On the other hand, the fact that eleven butterflies have been taken from the stomachs of western meadowlarks and that five different species of birds were found feeding on butterflies, to a greater or less extent, during an outbreak of these insects in northern California during the spring and summer of 1911 (Bryant, 1911), shows that butterflies are taken to some extent as food. The observational evidence of Mr. Tyler

already quoted (p. 430) also supports the latter statement. The ten pages of evidence given by Poulton (1908) also supports the view that birds, even though they do not feed to any considerable extent on these insects, do, occasionally at least, feed upon them. Mason and Lefroy (1912), after a study of the food of the birds of India, state: "Butterflies do not form any appreciable proportion of the food of any one species of bird, though a good many birds take these insects at times."

Although identification of the butterflies found in the stomachs has often been impossible, yet it is certain that they often belonged to separate families. The difference between the pierid butterfly, *Eurymus eurytheme,* and the nymphalid butterfly, *Eugonia californica,* is great enough to show that there is little choice shown. This evidence is supported by the work of Manders (1911). He concludes: "There is no bird in Ceylon known to eat butterflies that distinctly discriminates as an adult between one species of butterfly and another." Manders also goes so far as to say: "The fact that there is no discrimination shown by adults leads one to conclude either that few or no tasting experiments were undertaken in youth, or, what is more probable, that their taste with regard to them is indifferent." One important criticism that can be made of Mander's work is that he depended entirely on observation. The criticism bears less weight, however, since the insects under observation were of sufficient size and conspicuousness to make the observational method more dependable.

Any one who has watched a bird catch a butterfly must necessarily be impressed with the skill needed. Certain agility on the part of the butterfly must aid greatly in protecting it from attack. Further study may demand a change of emphasis from protective coloration to the protection afforded by the butterfly's ability to elude its pursuer.

There appears to be evidence that birds seldom attack butterflies, thus lending support to the theory that they are protected. On the other hand, it can be seen that there is evidence that butterflies are taken regularly as food by some birds. There are doubtless many factors which enter into the problem which have not as yet been considered. Hence until further evidence

is forthcoming the best conclusion would seem to be that birds occasionally eat butterflies, and that when they become extremely available the number taken is increased.

Spiny and hairy caterpillars have often been pointed out as specially well protected insects. At least fifty of the stomachs examined have contained these caterpillars. In one instance the larva of the mourning-cloak butterfly (*Euvanessa antiopa*) has been taken from a stomach. The size as well as the spiny character of this caterpillar would seem to preclude attack. Numbers of small hairy caterpillars have been taken from the stomachs. Judd (1899) states that "The hairiness of caterpillars seems to secure them from the attack of birds more effectually than do any of the protective devices so far considered." Comparing the relative abundance of these caterpillars available for the western meadowlark with those not so protected, it seems safe to say that certain of the smaller hairy caterpillars are not often passed by because of their hairiness.

Stink-bugs (Pentatomidae), in spite of their noxious secretion and disagreeable odor, form a constant article of diet for the western meadowlark. In the examination of a collection of birds from Newman, Stanislaus County, it was found that stink-bugs (*Euschistus, Podisus, Alydus, Coryzus*) had been taken every month from March to October, inclusive, and formed five and three-tenths per cent of the food for the year. Pinicate beetles (*Eleodes* sp.), having a noxious secretion, are commonly taken as food by meadowlarks.

Many stinging insects also form a constant article of diet. Chief among these are ants, bees and wasps, and cow-killers (Mutillidae). Kissing-bugs (Reduviidae) have been found in a few instances. The stomachs of two out of four birds eating reduviids were empty, indicating that the poison might have caused some discomfort. Bees and wasps are so often taken that it can hardly be said that their stinging propensities preclude attack. Probably their agility is much more important in protecting them from the attack of birds. Over two hundred ants have been taken from a single stomach. If the stings or the poison had any effect, it does not seem reasonable that a bird would feed exclusively on ants even when hard pressed for food.

The finding of scorpions in the stomachs of two meadowlarks from San Diego was a surprise for two reasons. Their size and sting would apparently protect them. In addition, their nocturnal habits and their habitat would seem to offer protection. That more were not taken is probably due to the fact that they are seldom available rather than that they are unpalatable.

The investigation has, therefore, shown that insects supposedly protected by noxious secretions, malodor, stings, etc., are taken as food by western meadowlarks. According to the old idea, the survival of these insects can be traced directly to protective adaptations. Early authors even suggested almost complete immunity from attack. In recent years this view has become modified. Judd (1899) called attention to the fact that "Biologists have not yet entirely elucidated all the details of the nature of adaptations of insects which are potently protected." The same thing can be said at the present time.

If we hold to the theory of natural selection, it is important that a certain toll be taken in order to perfect adaptation. If an insect had no enemies it would have little need of protective adaptations. Of course it may be argued that after the adaptation becomes perfected the enemies of insects learn to let them alone. Unless the variations were of the orthogenetic type, however, we could hardly expect such highly differentiated protective adaptations to exist as do exist. Kellogg's view that "success" is dependent on protective adaptations rests on this assumption. It overemphasizes the part played by protective adaptations. In the working of the principle of natural selection other principles and tendencies are working against the factor of protective adaptations, and it cannot be said that protective adaptations gain the ascendency over all other tendencies.

Unusual destruction of so-called protected insects and other arthropods can sometimes be attributed to young birds. Finn (1898) found out by experiment "that each bird has to separately acquire its experience, and well remembers what it has learned." Lloyd Morgan (1896) has also shown that birds have no instinctive knowledge of the different kinds of food, but that they examine and test everything. He also points out the fact that they have excellent memories and are able to remember suffi-

ciently so well any unpleasant sensation that they usually avoid a recurrence.

Under such circumstances, we should naturally expect that most of the birds taking protected insects, etc., would be young and inexperienced birds. In the present investigation juvenal birds have been differentiated from adults as far as possible. Consequently evidence on this point is available. Contrary to expectation, most of the birds taking protected insects and other arthropods as food have been adult birds. Their previous experience with this kind of food is unknown. The simplest explanation is to say that birds in searching for food take that at hand and that most easily obtained.

The only evidence afforded by this investigation that birds learn to let certain insects alone is the total lack of coccinellid beetles in the food of the western meadowlark. In California at certain times of year coccinellid beetles are extremely common and certainly would form an available food for the meadowlark if they were not protected from attack. The chrysomelid beetle, *Diabrotica soror*, a beetle sometimes confused with coccinellids, is occasionally taken as food. One stomach was found completely filled with these beetles. Hence it would seem that birds can distinguish between coccinellids which appear to be noxious and certain chrysomellids which appear to be edible. They also distinguish between pentatomids with a noxious secretion and coccinellids with a similar secretion.

Movement is a very important factor connected with the problem. Allen (1912) and Roosevelt (1911) have emphasized this point of view, that any coloration is protective only so long as the animal is motionless. Allen goes so far as to say that "coloration is a minor asset in an animal's protection in comparison with its other qualities—alertness, truculence and other traits that make for its protection." This point of view has received far less emphasis than its importance justifies.

The highest expression of vision is to be found in birds. The color sense, especially, is very acute, as shown by the preponderence of cones in the retinal elements. The range and rapidity of accommodation in birds far exceeds that of man or other animals, and the accommodative and refractive apparatus is much

more complex than in the other subkingdoms (Wood, 1907). Birds must, therefore, be able to distinguish readily the differently colored insects as well as to note quickly differences in size and any motion on their part. Hence the food taken must be largely the result of the reflex acts set up by the sight of food and much less as the result of studying each kind of food presented to determine its palatability. This brings us, of course, to "hunger" as one of the prime determining agents as to the kind as well as the amount of food taken.

Then, too, many insects and animals are protectively colored while at rest, but let them move and they immediately become conspicuous. Experiment has shown that most of the lower vertebrates depend largely on the movement of their prey to apprize them of its presence. A fly placed in a cage with horned lizards is unnoticed until it moves. Many a protectively colored insect must escape detection because it remains at rest. Let the same insect move and it is instantly detected.

Let us take a few examples in the food of the western meadowlark. Many of the snout-beetles (Otiorhynchidae) are inconspicuously colored and often so covered with dust as to be the exact color of the ground. Close search often fails to disclose a grasshopper on a grass-stem or weed, so well does it blend with its surroundings. The same can be said of stink-bugs. Yet all of these insects are taken in large numbers by meadowlarks. The explanation probably lies in this factor of movement. These insects, although well concealed while at rest, are not concealed when moving, but are, on the contrary, conspicuous.

An insect outside of its own environment is also easily detected by its enemies. A stink-bug, although inconspicuous on a green plant stem, becomes conspicuous on the bare ground. This again furnishes a possible reason for the large numbers of these insects found in the stomachs of western meadowlarks.

Movement and particular environment modify the value of protective or concealing coloration. There may also be still other factors which modify its value. Size and bright coloration must add to an insect's conspicuousness in both movement and change of environment. All evidence from this investigation points to the fact that although certain insects may be protectively colored,

yet they are not immune from the attack of birds because of such coloration. The fact that protective coloration is of maximum utility to the insect only when it is at rest, and of minimum utility when it is moving or when it is out of its natural habitat, in a large measure explains the occurrence of these insects in the food of birds.

Cow-killers (Mutillidae) have been found in several instances. These insects are usually considered as being warningly colored. Were they as abundant as other insects the numbers taken by western meadowlarks would be insignificant. In that they are not numerous, the fact that five stomachs contained them indicates that their warning coloration did not protect them wholly from attack.

It may even be said that certain unpalatable insects are taken as food simply because they are made conspicuous by movement, thus setting up a chain of reflexes in the bird which result in their being eaten. The reflexes set up by the stimulus of the sight of food play an important part in determining the kind and amount of food taken. A bird feeding on grasshoppers would doubtless be more greatly influenced by the sight of another grasshopper than by that of a small beetle or even a cricket the same size as the grasshopper. The psychological process involved in the feeding habit has been little studied. Its importance as a factor suggests this as a fruitful source from which might come illuminating evidence on the problem.

Availability as a Factor in the Kind and Quantity of Food

Western meadowlarks collected in grain fields appear to take as food practically every kind of insect and other arthropod to be found in grain fields. Small size does not govern the kind of food, for one bird was found to have eaten aphids. Nor, on the other hand, does large size preclude attack, for pinicate beetles (*Eleodes* sp.) are eaten. Insects with stings, such as ants, bees, and wasps, insects with noxious secretions, such as stink-bugs, and even hairy caterpillars are regularly taken as food. The respective quantity of each kind taken appears to parallel their abundance and accessibility. The term *availability* denotes the

totality of factors governing the food-taking of birds. In other words, in spite of the fact that birds select food to a greater extent than many other animals, they do not select kinds or quantities of food elements to the degree to which we have been led to believe from experiments on captive birds, but are governed more largely by the abundance, the ease of capture, the conspicuousness, etc., of the insect, or, in other words, its availability.

The attempt has been made heretofore to interpret the food habits of birds from the standpoint of the insect, an endeavor being made to show why certain insects were not taken as food. Looking at the same problem from the standpoint of the bird, we can say that with few exceptions the term *availability*, when defined as above, best expresses the interrelations associated with the food habits of birds. Under this term can be grouped both the objective factors concerned, such as abundance, ease of capture, conspicuousness, etc., and the psychological factors involved in the taking of food.

SOLVED AND UNSOLVED PROBLEMS IN ECONOMIC ORNITHOLOGY

In spite of the advance made in the study of the food of birds and their relation to agriculture, there are still many problems connected with economic ornithology that are still unsolved.

Great improvement in the technique of determining the food of birds has been achieved. The modern method of stomach examination combined with field observation is so far ahead of the former method of simple observation or inferential reasoning that one is led to believe that a solution of many of the problems presented is near at hand. The criteria used in determining the status of a bird have also been improved to such an extent that were it possible to obtain the prescribed kind of evidence our estimates of the value of a bird must needs be near the truth.

Our goal, "a balance of all the benefits conferred against all the injuries inflicted," is a fine ideal, but we are still unable to attain it. A great deal is still made of the fact that certain birds eat large quantities of injurious insects. Yet what are injurious insects? Insects injurious in one place may be comparatively

unimportant in another place. Abundance even more than the kind of an insect appears to govern its injuriousness. Hence the direct value of the destruction of certain insects by birds is difficult to estimate.

The solution of the problem lies in a determination of the comparative abundance of insects. The censuses of birds taken by Forbes (1901) in Illinois have been of incalculable value to ornithologists and everyone regrets the lack of others of the same type. The entomologist has left this quantitative phase almost wholly untouched. Consequently the economic ornithologist, in attempting to determine the good accomplished by birds in destroying insects, has no evidence on which he can depend as to the comparative numbers of the insects upon which they feed. The difficulty of obtaining any exact idea of the numbers of a species of insect in the field is very great, but the importance and value of the information will certainly repay effort made in this direction. Economic ornithologists must necessarily await data of this kind before they will be able to point out conclusively the importance to be attached to the destruction of insects by birds.

In years past we have been wont to judge the value of a bird entirely on its food. The present tendency to regard the food habit as only one of the things to be considered in judging its value is an advance worthy of note. The esthetic value is fast coming to be appreciated by every one. It must certainly be given an important place in any adequate estimate of a bird's value.

In a broad sense food preference furnishes evidence as to the value of a bird. For instance, a bird that eats insects can be considered of more value to the agriculturist than one that subsists entirely on vegetable food. To particularize and say that a bird prefers a certain kind of insect is to tread on dangerous ground, for birds appear to be governed more largely by the abundance of an insect than by its taste. The opportunity afforded a bird for obtaining an insect appears to be a stronger factor than memory of a bad taste. Consequently the old idea of food preference must be modified to meet the modern idea of availability as a factor in the kind and quantity of food.

The exact relation which birds bear to the control of insect outbreaks remains to be worked out. There are a number of factors which tend to bring back normal conditions. Whether birds, parasitic insects, weather conditions, or other factors are of prime importance is a problem yet to be solved. The beginning has been made and significant evidence adduced. A comprehensive study of this problem would do much towards solving it.

The amount of benefit to be derived through the destruction of weed seeds is still a debated question. When such efficient measures as the weed cutter and the mowing machine can be brought into use, the amount of good accomplished in a bird's destruction of weed seeds is minimized. A weed-seed eater must be considered a less valuable bird than an insect eater where weeds are more easily controlled than insects. Better insect control measures will likewise make the value of insectivorous birds less apparent. The inherent value, nevertheless, remains unchanged. Common sense would seem to dictate the making use of natural control measures to the greatest extent possible. Herein lies the justification for emphasis on the value of birds as insect and weed-seed destroyers.

SUMMARY

Owing to the constant complaint of ranchers as to the depredations of birds and attempted legislation to take protection away from certain non-game birds, the California State Fish and Game Commission, in co-operation with the University of California, has undertaken a thorough, scientific investigation into the relations of birds to agricultural interests. The western meadowlark (*Sturnella neglecta*), owing to its depredations in sprouting grain fields, has been the first bird to be studied.

A study of the history of methods used in economic ornithology has shown that the time has come when circumstantial or partial evidence as to the food of a bird is insufficient evidence on which to determine its economic status. Nothing short of a knowledge of a bird's food for the whole year, a knowledge of its depredations, and its whole life history, allowing a balance of all of the benefits conferred against all of the injuries done, is now demanded.

The western meadowlark is distributed throughout the state, most abundantly in the great interior valleys, the grain-growing districts. It appears to be increasing in numbers in localities where cultivated crops are furnishing it better food and cover.

The investigation has included field investigation of birds at the field of action, experimentation on the amounts of food consumed and the times of digestion, and stomach examinations of the kinds and quantities of food actually consumed.

Over twenty collections from different parts of the state, made up of birds collected each month of the year in the same general locality, have been available for stomach examination. Nearly two thousand stomachs of western meadowlarks have been examined and the kind and quantity of the different elements of food tabulated.

Field investigation has shown that the western meadowlark destroys sprouting grain by boring down beside the sprout and eating the kernel. The amount of damage depends upon the abundance of the birds, the depth to which the grain is planted, the size of the field, the condition of the soil, the proximity to pasture or uncultivated land, and the time of year. The amount of damage possible is minimized by the short time (two weeks) during which damage to the young plant can result. No other crops are seriously damaged by western meadowlarks. Young meadowlarks are fed exclusively on insect food, principally cutworms and grasshoppers.

Experimentation on captive birds has shown that nestling birds consume very nearly their own weight of food every day. The time during which insects remain in the stomach is from three to four hours. The time during which grain remains in the stomach is from four to six hours. Hence the time of digestion of grain is longer than that of insects. The amount of insect food found in the stomach of a western meadowlark represents, therefore, but one-third of the daily requirement.

Stomach examination has shown that sixty-three and three-tenths per cent of the total volume of food of the western meadowlark for the year is made up of animal matter and thirty-six and seven-tenths per cent of vegetable matter. The animal matter is made up mostly of ground beetles, grasshoppers, crickets, cut-

worms, caterpillars, wireworms, stink-bugs, and ants, insects most of which are injurious to crops. The vegetable matter is made up of grain and seeds. Grain as food reaches a maximum in November, December, and January, insects in the spring and summer months, and weed seeds in September and October. An average stomach of a western meadowlark contains two and three-fourths cubic centimeters of food. The kind and quantity of food varies with the time of year and locality.

A study of the relation of birds to insects has shown that birds are important regulators of the numbers of insects for at least two reasons: (1) the maximum consumption of insects comes during the nesting season of birds, a time when the numbers of insects are at a maximum; (2) birds change their food habits and feed on the insect most available, thereby becoming important balancers during insect outbreaks when insects appear in abnormal numbers.

The verdict of ranchers throughout the state obtained by a circular letter has shown that there is a wide difference of opinion as to the extent of damage caused by the western meadowlark. A majority maintain that this bird does not damage crops and is, therefore, not a nuisance.

A comparison of the injuries caused by the western meadowlark with the benefits it confers shows that it does more good than harm, and so merits protection as an insectivorous non-game bird. Crops may be largely protected by drilling grain deeply or by furnishing the birds sufficient food by heavier sowing.

The examination of so large a number of birds of one species has furnished some interesting side-lights on the investigation. Evidence on such biological problems as parasitism, malformation, albinism, natural death rate, etc., has been made available.

Protective adaptations of insects do not render them immune from the attack of birds. This investigation has demonstrated the following facts bearing on the relation of birds to insects with protective adaptations:

1. Protective adaptations of arthropods such as stings, noxious secretions, hairs, etc., have been overemphasized as factors protecting the owners from the attack of birds.

2. The "availability" of an insect or arthropod, when this term is made to include the totality of factors governing the

taking of an insect by a bird, can be considered the most potent factor governing the food habits of birds.

3. Hunger or inexperience fails to account for the destruction of many of the so-called protected insects, because in many instances they form staple articles of diet.

4. The fact that coccinellid beetles almost wholly escape the attack of birds is the one thing that supports the theory that certain arthropods are practically immune from the attack of birds in spite of the fact that they are available as food. The logical explanation of the immunity lies in the possession of a noxious secretion which makes them unpalatable. Why this secretion should be more effective than that of the Pentatomidae or certain tenebrionid beetles is not known.

5. Insects protectively colored when at rest are easily detected by birds or other enemies as soon as they move. An insect outside of its natural habitat also becomes easy to detect. These factors of movement and change of habitat may explain the occurrence of certain protectively colored insects in the diet of the western meadowlark.

6. The reflexes set up by the stimulus of the sight of food, or, in other words, the psychological processes involved in the taking of food, doubtless play an important part in the kind and quantity of food taken.

A number of factors govern the kind and amount of food taken by birds. The totality of such factors (e.g., abundance, palatability, ease of capture, conspicuousness, etc.) can be expressed by the term *availability*. *Availability*, thus used, best accounts for the varying food habits of birds.

Although great progress has been made in economic ornithology, there are still a number of problems that remain unsolved, chief of which is the value to be placed on the destruction of insects and weed seeds effected by birds. Since a solution of this problem depends upon quantitative studies of the comparative abundance of different species of insects and weed seeds, economic ornithology must await such studies from the entomologist and botanist.

Transmitted May 2, 1913.

BIBLIOGRAPHY

N. B.—For papers on economic ornithology previous to 1901 see Weed (1902). For publications of the United States Biological Survey see McAtee (1913).

Allen, C. N.

1881. Songs of the western meadowlark. Nutt. Orn. Club. Bull., **6**, 145–150.

Allen, J. A.

1876. Progress in ornithology in the United States during the last century. Amer. Nat., **10**, 536–550.

1881. Insectivorous birds in their relation to man. Nutt. Orn. Club. Bull., **6**, 22–27.

1912. Remarks on the case of Roosevelt vs. Thayer, with a few independent suggestions on the concealing coloration question. Auk, **29**, 489–507.

Anonymous.

1909. The true function of birds. Sci. Amer. S., **68**, 266–267.

1910. The control of the Argentine ant. Univ. of Calif. Publ., Agric. Exp. Sta. Bull., **207**, 51–82, 28 figs. in text.

1911. Consider the birds of the air. Craftsman, **21**, 372–421.

Archibald, C. F.

1907. Wild birds, useful and injurious. Jour. Royal Agric. Soc. Eng., **68**, 17–32, 7 figs. in text.

Audubon, J. J.

1831–39. Ornithological biography (A. Black, Edinburgh), 5 vols., many woodcuts in text.

Aughey, S.

1878. Notes on the nature of the food of birds of Nebraska. U. S. Entom. Comm., First Rep., Append. 2, pp. 13–62.

Baer, W.

1909. Untersuchungsergebnisse von Mageninhalt sächsischen Vögel. Ornith. Monatschr. Magdeburg, **34**, 33–34.

Baskett, J. N.

1910. Birds and insect pests. Sci. Amer., **103**, 379.

Barrows, W. B.

1912. Michigan bird life (Mich. Agric. College, Lansing, Mich.), xiv + 822, 70 pls., 151 figs. in text.

Beal, F. E. L.

1894. The meadowlark and Baltimore oriole. U. S. Dept. Agric. Yearbook, **1894**, 419–430, 2 figs. in text.

1897. Revent investigations of the food of European birds. Auk, **14**, 8–14.

1906. Birds as conservators of the forest. State of N. Y. Forest, Fish, and Game Comm. Rep., **1902-1903**, 236–274, 14 pls.

1907. Birds of California in relation to the fruit industry. Part I, U. S. Dept. Agric., Div. Biol. Surv. Bull., **30**, 1–100, 5 pls.

1908. The relations between birds and insects. U. S. Dept. Agric. Yearbook, **1908**, 343–350.

1910. Birds of California in relation to the fruit industry. Part II, U. S. Dept. Agric., Div. Biol. Surv. Bull., 34, 1–96, 6 pls.

1912. Food of our more important flycatchers. U. S. Dept. Agric. Bur. Biol. Surv. Bull., 44, 1–67, 5 pls.

Beebe, C. W.

1906a. The bird (Henry Holt & Co., N. Y.), xi + 496, 371 figs. in text. The food of birds, pp. 142–164.

1906b. Oddities of bird diet. Outing, 47, 227–228.

Bendire, C. E.

1892. Life-histories of North American birds. Smithson. Inst. Contrib. Knowl., 1, ix + 445, 12 pls.

1895. Life-histories of North American birds. *Ibid.*, 2, ix + 518, 7 pls.

Blanchan, N.

1903. How to attract the birds (Doubleday, Page & Co., N. Y.), 1–224, many figs. in text.

Bowdish, B. S.

1906. The rapid growth of birds. Sci. Amer. S., 61, 25373–25374.

Bryant, H. C.

1911. The relation of birds to an insect outbreak in northern California during the spring and summer of 1911. Condor, 13, 195–208, 4 figs. in text.

1912a. The economic status of the meadowlark in California. Mon. Bull. State Comm. Hort. (Sacramento, Calif.), 1, 226–231, 2 figs. in text, 2 tables.

1912b. The Lewis woodpecker—A destroyer of almonds. *Ibid.*, 1, 362–366, 2 figs. in text.

1912c. Native birds and mammals. Western Field (Los Angeles, Calif.), 19, 432–435, 2 figs. in text.

1912d. Birds in relation to a grasshopper outbreak in California. Univ. Calif. Publ. Zool., 11, 1–20.

1912e. Some insects and other arthropods in the diet of the western meadowlark. Pomona College Jour. Entomology (Claremont, Calif.), 4, 807–809.

1912f. The numbers of insects destroyed by western meadowlarks (*Sturnella neglecta*). Science, 36, 873–875.

1913a. Why non-game birds should be protected. Western Wild Life Call (Pub. by Calif. Associated Societies for the Conservation of Wild Life, Berkeley, Calif.), no. 1, pp. 8–11, 4 figs. in text.

1913b. The economic value of the western meadowlark in California. Univ. Calif. Publ., Agric. Exp. Sta. Bull., 236, 1–16, 7 figs. in text.

1913c. Investigation of the economic status of non-game birds. Reprint from Game Bull. no. 1, Calif. State Fish and Game Comm. (State Printing Office, Sacramento, Calif.), 1–19, 8 figs. in text.

1913d. The results of some miscellaneous stomach examinations. The Condor, 15, 92.

Bryant, W. E.

1893. Notes on the food of birds. Zoe, 4, 54–58.

Chapman, F. M.
1903. The economic value of birds to the state. State of New York Forest, Fish, and Game Comm., **1903**, 1–66, 12 pls.
1907. Bird life (Appleton & Co., N. Y.), xii + 88, 75 pls., 25 figs. in text.
1908. Camps and cruises of an ornithologist (Appleton & Co., N. Y.), xvi + 432, illus.
1909. A study of the genus *Sturnella*. Amer. Mus. Nat. Hist. Bull., **13**, 297–320, 8 figs. in text.

Chernelhaza, S. C. von
1909. Beiträge zur Nahrungsfrage unserer carnivoren Vogelwelt. Aquila, Budapest, **16**, 145–155.

Cleland, J. B.
1910. Examination of contents of stomachs and crops of some Australian birds. Emu, **9**, 219–226. Agric. Gaz. N. S. Wales, **21**, 73–156.

Collinge, W. E.
1912. The food of nestling birds. Jour. Bd. Agric., London, **19**, 460-465.

Coues, E.
1874. Birds of the northwest (Gov. Printing Office, Washington), U. S. Geol. Surv. of Terr., Misc. Publ., **3**, xi + 791.

Coward, T. A.
1912. The migration of birds (Univ. Press, Cambridge; G. P. Putnams Sons, N. Y.), 1–137, 4 maps.

Cowan, J. C.
1911. Refuges for birds. Overland, **57**, 637–642.

Crary, L. E.
1911. A text-book of field zoology (Blakiston's Sons & Co., Phila., Pa.), 1–364, 117 figs. in text.

Csiki, E.
1909. Positive Daten über die Nahrung unserer Vögel. Aquila, Budapest, **16**, 139–144.

Daehne
1909. Schmetterlingsfeinde aus der Klasse der Vögel. Zs. Naturw., Stuttgart, **81**, 184–187.

Dawson, W. Leon, and Bowles, J. H.
1909. The birds of Washington (Occidental Publ. Co., Seattle, Wash., 2 vols., xv + 997, 44 pls., 300 figs. in text.

Dewar, D., and Finn, F.
1909. The making of species (J. Lane & Co., N. R.), xix + 400, 10 pls.

Dugmore, A. R.
1907. Birds as insect destroyers. Country Life, **11**, 384–390.

Dutcher, Wm.
1904. Report of the A. O. U. committee on the protection of North American birds and of the national committee of Audubon societies. Auk, **21**, Supp., 97–208.

Elliot, D. C.
1864. The game birds of the United States. U. S. Dept. Agric. Rep., **1864**, 356–385, 5 pls.
Finley, W. L.
1907. American birds (Chas. Scribner's Sons, N. Y.), xvi + 256, 127 figs. in text.
1909. Study of birds and their economic value: Some common birds of Oregon. Fourth Biennial Report of the State Biologist of Oregon, Append., pp. 3–24.
Fisher, A. K.
1887. Food of hawks and owls. U. S. Dept. Agric., Ann. Report, **1887**, 402–422.
1893. The hawks and owls of the United States in their relation to agriculture. U. S. Dept. Agric., Div. Biol. Surv. Bull., **3**, 1–210, 26 pls.
Flagg, W.
1862. Utility of birds. Mass. Agric. Rep., **1861**, 70–78.
Florence, L.
1912. The food of birds. Trans. Highland, and Agric. Soc. Scotland, **24**, 180–219.
Folsom, J. W.
1909. Entomology with especial reference to its biological and economic aspects (P. Blakiston's Sons & Co., Phila., Pa.), vii + 485, 5 pls., 300 figs. in text.
Forbes, S. A.
1880. On some interactions of organisms. Bull. Ill. State Lab. Nat. Hist., **1**, 3–17.
1882. The ornithological balance-wheel. Trans. Ill. State Hort. Soc., new ser., **15**, 120–131.
1885. The regulative action of birds upon insect oscillations. Ill. State Lab. Nat. Hist. Bull., **1**, 3–32.
1903. The food of birds. *Ibid.*, **1**, 86–161.
1907. An ornithological cross-section of Illinois. *Ibid.*, **7**, 305–335, 12 tables.
1908. The midsummer bird life of Illinois: A statistical study. Amer. Nat., **42**, 505–519.
Forbush, E. H.
1908a. Birds as protectors of orchards. Mass. State Bd. Agric. Bull., July, 1895, 1–19.
1908b. Two years with the birds on a farm. *Ibid.*, June, 1908, 1–44, 8 figs.
1908c. Useful birds and their protection (3rd ed., Mass. State Bd. of Agric., Boston), xx + 437, 56 pls., 171 figs. in text.
1910. Third annual report of the State Ornithologist. Mass. State Bd. of Agric. Rep., **58**, 167–197.
Gaut, H. L.
1906. What do birds eat? Sci. Amer., **95**, 379.
Gentry, T. G.
1876. Life-histories of the birds of Pennsylvania (Pub. by the author, Phila.), vol. 2, xiv + 399.

Gilmour, John

1896. Bird investigation: An inquiry concerning the relation of certain birds to the agricultural interest, as shown by their diet. Jour. Highland. Agric. Soc., **1896**, 21–112.

Gladden, Geo.

1912. Shall Uncle Sam protect the birds. Amer. Rev. of Rev., **46**, 705–715, 20 figs. in text.

Gossard, H. A.

1908. Spring practice in economic zoology. Ohio Agric. Exp. Sta. Bull., **198**, 15–88, Appendix viii.

Greschik, Eugen

1910. Magen- und Gewölluntersuchungen unserer unheimischen Raubvögel. I. Mitteilung. Aquila, **17**, 1–13.

1911. II. Eulen. *Ibid.*, **18**, 111–177, 6 figs. in text.

Gunning, J. W.

1908. Locusts birds. Transvaal Agric. Jour., **6**, 527–530.

Hammond, John

1912. An investigation concerning the food of certain birds. Jour. of Agric. Soc. London, **4**, 380–407.

Henderson, J.

1913. The practical value of birds. Univ. of Colo. Bull., **13**, 1–48.

Henshaw, H. W.

1907. Does it pay the farmer to protect the birds? U. S. Dept. Agric. Rep., **1907**, 165–178.

1908. The policemen of the air: An account of the Biological Survey of the Department of Agriculture. Nat. Geog. Mag., **19**, 79–118, 38 figs. in text.

Hewitt, C. G.

1909. An inquiry into the feeding habits of British birds. British Ass. Adv. Sci. Rep., **1908**, 734–735.

Hollrung, M.

1906. Beiträge zur Bewertung der Saatkrähe auf Grund von 11-jahrigen Magenuntersuchungen. Landwirtschaft. Jahrb. **35**, 579–620, 1 fig. in text.

Holmes, E.

1857. Birds injurious to agriculture. Rep. U. S. Patent Office, Agric., **1856, 1857**, 110–160, pls. 15–46.

Hooper, C. H.

1908. The commoner birds of our gardens, their habits and food. Jour. Royal Hort. Soc. London, **33**, 427–450, 1 fig. in text.

Hornaday, W. T.

1913. Our vanishing wild life (Chas. Scribner's Sons, N. Y.), xv + 411, many illus. The economic value of birds, pp. 211–233.

Jenks, J. W. P.

1860. The food of the robin. Jour. Proc. Mass. Hort. Soc., **1859**, 151–154.

JUDD, S. D.
1897. Methods in economic ornithology, with especial reference to the catbird. Amer. Nat., **31**, 392–397.
1899. The efficiency of some protective adaptations in securing insects from birds. *Ibid.*, **33**, 461–484.
1900. Food of nestling birds. U. S. Dept. Agric. Yearbook, **1900**, 411-436.
1901. The relation of sparrows to agriculture. U. S. Dept. Agric., Div. Biol. Surv. Bull., **15**, 1–98, 4 pls., 19 figs. in text.
1902. Birds of a Maryland farm. *Ibid.*, **17**, 1–116, 16 pls., 41 figs. in text.

KALBFUS, JOSEPH
1911. Wild bird protection. Penn. State Bd. of Game Comm. Bull., **2**, 1–23, 12 figs. in text.

KELLOGG, V. L.
1908. American insects (Holt & Co., N. Y.), xiv + 694, 812 figs. in text.

KING, F. H.
1883. Economic relations of Wisconsin birds. Geology of Wis., **1**, 441–610, 41 figs. in text.

KIRBY, WM., and SPENCE, WM.
1858. An introduction to entomology (7th ed., Longman, Brown, Green, Longmans, and Roberts, London), xxviii + 607. Interaction of organisms, p. 145.

KNIGHT, W. C.
1902. The birds of Wyoming. Wyo. Agric. Exp. Sta. Bull., **55**, 1–174.

LEISEWITZ, W.
1906. Untersuchungen über den Nahrung einiger land- und forstwirtschaftlich wichtigen Vögelarten. Verhand. der Orn. Gesellschaft in Bayern, **6**, 194–203.
1907. Ueber neuere Untersuchungen zur Kenntnis der Nahrung der Vögel. *Ibid.*, **7**, 265–274.
1911. Untersuchungen des Inhalts von Raubvögelmagen. *Ibid.*, **10**, 156–182.

LE BARON, W.
1855. Observations upon some of the birds of Illinois most interesting to the agriculturist. Trans. Ill. State Agric. Soc., **1853-1854**, 559–565.

LOCY, W. A.
1910. Biology and its makers (Henry Holt & Co., N. Y.), xxvi + 469, 123 figs. in text.

MASON, C. W., and LEFROY, H. M.
1912. Preliminary report on food of Indian birds. Mem. Dept. Agric. India, Entom. Ser., **3**, 1–371.

MCATEE, W. L.
1906. A buried treasure of economic ornithology. Sci., **24**, 308–312.
1912a. The experimental method of testing the efficiency of warning and cryptic coloration in protecting animals from their enemies. Proc. Acad. Nat. Sci. Phila., **1912**, 281–364.

1912b. Methods of estimating the contents of bird stomachs. Auk, **29**, 449–464.

1912c. Review of Bryant's "The relation of birds to an insect outbreak in northern California during the spring and summer of 1911. Condor, **14**, 45–46.

1913. Index to papers relating to the food of birds. U. S. Dept. Agric., Bur. Biol. Surv. Bull., **43**, 1–69.

Merriam, T. A.

1896. How birds effect the farm and garden. Forest and Stream, **47**, 103, 123, 141.

Minot, Chas. A.

1911. The method of science. Sci., **33**, 119–131.

Nash, Chas. W.

1909. The birds of Ontario in relation to agriculture. (4th ed.), Ont. Dept. Agric. Bull., **173**, 1–75, pls.

Peabody, P. B.

1897. Song notes and nesting habits of the western meadowlark. Osprey, **1**, 139–141, 1 fig. in text.

Palmer, T. S.

1899. A review of economic ornithology. U. S. Dept. Agric. Yearbook, **1899**, 259–292.

Pearson, T. G.

1909. Some common birds on the farm. N. C. Dept. Agric., Special Bull., Supp. Sept. Bull., **1909**, 1–28, 5 figs. in text.

1913. Economic value of birds. Craftsman, **23**, 432–438.

Pennock, Chas. J.

1904. Some of our useful birds. Dela. State Bd. of Agric. Bull., **5**, 1–16, 6 figs. in text.

Perris, E.

1880. Birds vs. insects. (Translated by S. A. Forbes.) Amer. Entom., **1**, 69–72, 96–100.

Pocock, R. I.

1893. Further notes and observations on the instincts of some common English spiders. Nature, **49**, 61–63.

Poulton, E. B.

1887. The experimental proof of the protective value of color and color markings in insects in reference to their vertebrate enemies. Proc. Zool. Soc. London, **1887**, 191–274, 5 tables.

1890. The colors of animals (Kegan Paul, Trench, Trübner & Co., London), xiii + 360.

1898. Natural selection, the cause of mimetic resemblance and common warning colors. Jour. Linn. Soc. London, Zool. Ser., **26**, 558–612, pls. 40–44.

1908. Essays on evolution (Clarendon Press, Oxford), xlviii + 479.

Praeger, Wm. E.

1899. Birds in horticulture. Trans. Ill. State Hort. Soc., New Ser., **33**, 1–11.

PREVOST, M. F.
1858. A memoir on the alimentary regimen of birds presented to the Imperial Zoological Society of Paris. (Translated by J. W. P. Jenks.) Trans. Mass. Hort. Soc., 1859, 109–114.

PYCRAFT, W. P.
1910. A history of birds (Methuen Co., London), xxxi + 458, 36 pls., 50 figs. in text.

ROGERS, J. E.
1910. Birds that save our crops. Country Life, 18, 250–254.

ROOSEVELT, T.
1911. Revealing and concealing coloration in birds and mammals. Amer. Mus. Nat. Hist. Bull., 30, 119–231.

RÖRIG, G.
1903a. Studien über die wirtschaftlichen Bedeutung der insekton-fressenden Vögel. Berlin Arb. biol. Anst., 4, 1–50.
1903b. Untersuchungen über die Nahrung unserer heimischen Vögel mit besonderer Berücksichtigung der Tag- und Nachtraubvögel. *Ibid.*, 51–120, 3 Tafeln.
1909. Magen- und Gewölluntersuchungen heimischen Raubvögel. Berlin biol. Anst., 7, 473–520.

SAMPLE, O. H.
1910. The conservation of birds. Outlook, 95, 669–676, illus.

SCLATER, W. L.
1912. A history of the birds of Colorado (Witherby & Co., London), xxiv + 576, 16 pls., 1 map.

SHUFELDT, R. W.
1887. On the skeleton in the genus *Sturnella*, with osteological notes upon other North American Icteridae and the Corvidae. Jour. of Anat. and Physiol., 22, 309–350, 2 pls.

SURFACE, H. A.
1908. Birds and horticulturists. Penn. State Dept. Agric., Mon. Bull. Div. of Zool., 5, 299–320, 3 pls., 7 figs. in text.
1905. The economic value of our native birds. *Ibid.*, 3, 240–267, 6 pls.

SULLIVAN, R. H.
1910. The economic value of bird life. Agric. Educ., 3, 1–47, 30 figs. in text.

SWYNNERTON, C. F. M.
1912. Remarks on the stomach contents of birds. Ibis, 6, 635–640.

TITCHENER, E. B., and FINN, F.
1889. Comparative palatability of insects, etc. Nature, 42, 571–572.
1891. *Ibid.*, 44, 540.
1892. *Ibid.*, 45, 53.

THEOBALD, F. V.
1908. Economic ornithology in relation to agriculture, horticulture, and forestry. Sci. Progress, 2, 263–283.

TREADWELL, D.
1859. The food of young robins. Proc. Boston Soc. Nat. Hist., 6, 396–399. Review U. S. Patent Office Rep. on Agric., 1860, 88–89.

Warren, B. H.
1888. Report of the birds of Pennsylvania (E. K. Meyers, Harrisburg, Pa.), xii + 260, 50 pls.

Weed, C. M.
1902. A partial bibliography of the economic relations of North American birds. N. H. College Agric. Exp. Sta. Tech. Bull., 5, 139–179.
1910. Farm friends and farm foes (D. C. Heath & Co., Boston, Mass.), xi + 334, 1 map, 160 figs. in text.

Weed, C. M., and Dearborn, N.
1903. Birds in their relation to man (Lippincott, Phila., Pa.), viii + 380, illus.

Wheelock, I. G.
1905. Regurgitative feeding of nestlings. Auk, 22, 54–71.
1906. Nesting habits of the green heron. *Ibid.*, 23, 432–436.

Wier, J. J.
1869. On some insects and insectivorous birds, and especially on the relation between color and the edibility of Lepidoptera and their larvae. Trans. Ent. Soc. London, **1869**, 21–26.

Wilcox, E. V.
1892. The food of the robin. Ohio Agric. Exp. Sta. Bull., **43**, 115-131.

Wilson, A.
1808–14. American Ornithology (Bradford & Inskeep, Phila., Pa.), 9 vols., many pls. and figs.

Woodworth, C. W.
1902. Grasshoppers in California. Univ. of Calif. Publ., Agric. Exp. Sta. Bull., 142, 1–36, 17 figs. in text.
1903. A list of the insects of California. (Pub. by the author, Berkeley, Calif.), pp. 1–80.

EXPLANATION OF PLATES

PLATE 21

Fig. 1.—Holes bored by western meadowlarks in obtaining kernels of grain in sprouting grain field. Photograph by H. C. Bryant taken at Lathrop, San Joaquin County, California, February 28, 1912.

Fig. 2.—Sprouted grain pulled up by western meadowlarks in grain fields at Acampo and Lathrop, San Joaquin County, California. The kernels have been crushed in the bill to obtain the "milk".

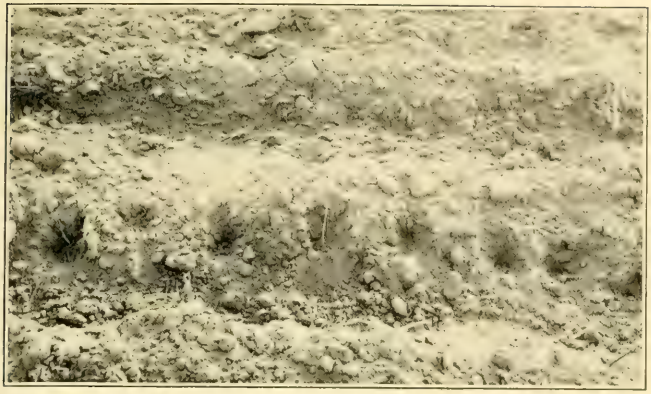


Fig. 1

Fig. 2

PLATE 22

Fig. 3.—Photograph of the stomach contents of a western meadowlark taken in a grain field at El Toro, Orange County, California, May 5, 1911. The stomach contained 19 oat kernels, oat hulls, and parts of 2 small ground beetles.

Fig. 4.—Photograph of twelve pairs of mandibles of the common cricket (*Gryllus pennsylvanicus*) taken from the stomach of a western meadowlark collected in a grain field at El Toro, Orange County, California, April 18, 1911.

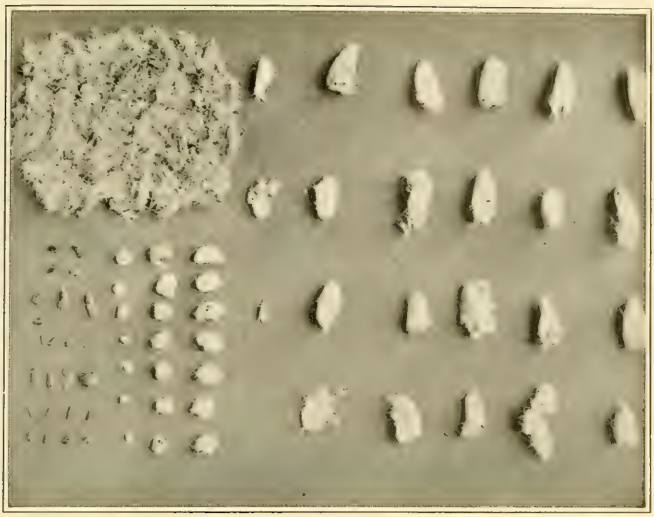


Fig. 3

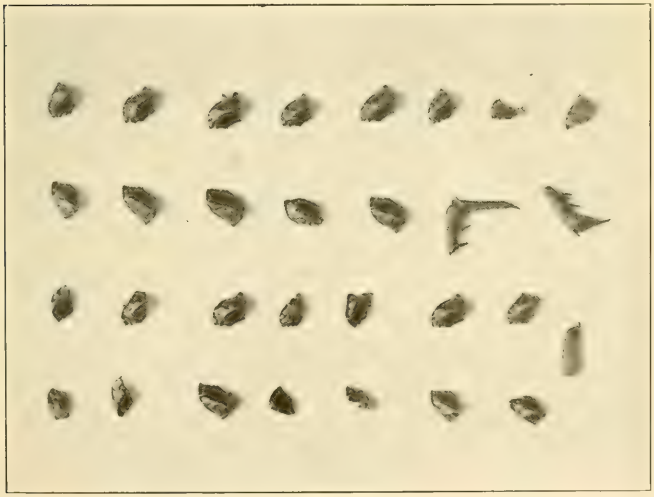


Fig. 4

PLATE 23

Fig. 5.—Photograph of the stomach contents of a western meadowlark taken at Red Bluff, Tehama County, California, February 4, 1911. Stomach contained 66 cutworms, 18 small ground beetles, 2 beetle larvae, 2 small spiders, and 18 weed seeds.

Fig. 6.—Photograph of western meadowlark killed while carrying cutworms in its bill.

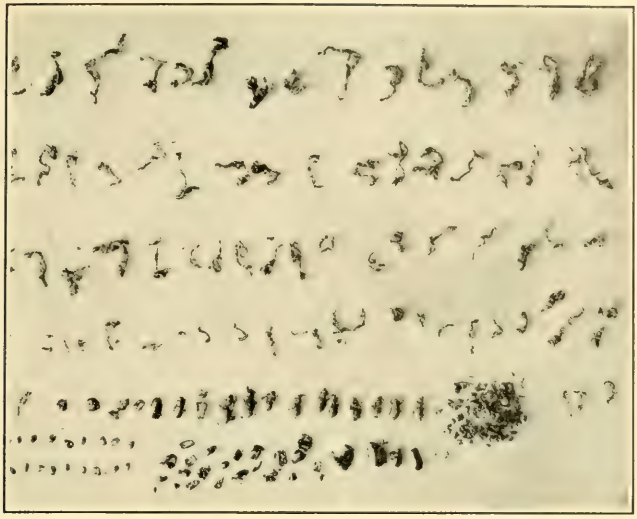


Fig. 5

Fig. 6

PLATE 24

Fig. 7.—Photograph of stomach contents of a western meadowlark taken in a barley field at El Toro, Orange County, California, May 3, 1911. The stomach contained 2 cutworms, 44 ground beetles (*Calathus ruficollis*), 2 flies, 1 spider, and 13 fly pupae (*Syrphus* sp.).

Fig. 8.—Photograph of the stomach contents of a western meadowlark collected at Big Pine, Inyo County, California, April 19, 1911. The stomach contained 13 cutworms, 26 elaterid beetles (*Drasterius* sp.), and 10 small ground beetles (*Amara* sp.).

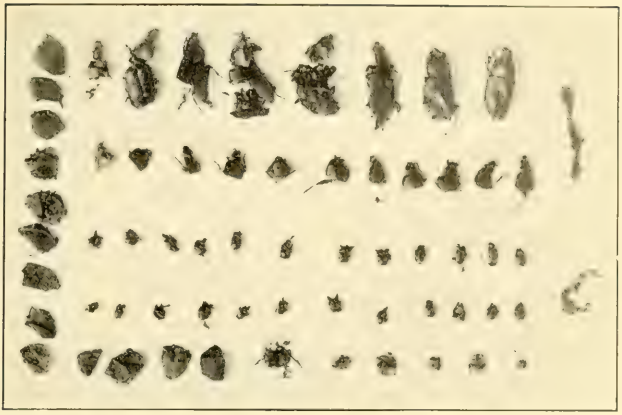


Fig. 7

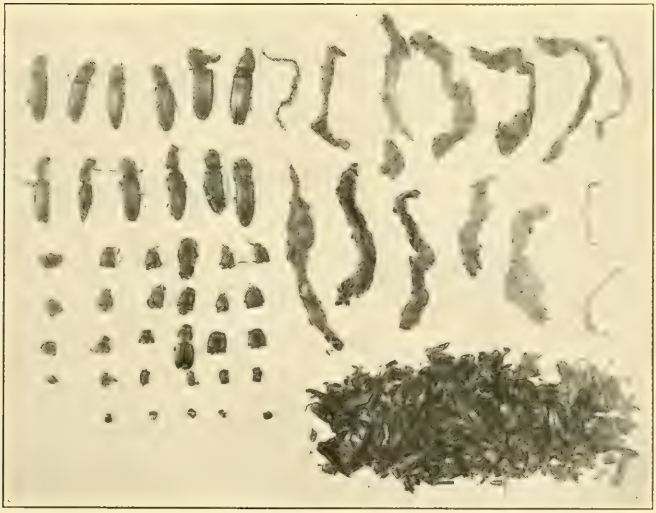


Fig. 8

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY
Vol. 11, No. 15, pp. 511-528, pls. 25-26, 1 text fig. April 15, 1914

PARASYNAPTIC STAGES IN THE TESTIS OF *ANEIDES LUGUBRIS* (HALLOWELL)

BY
HARRY JAMES SNOOK AND J. A. LONG

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY

UNIVERSITY OF CALIFORNIA PUBLICATIONS

Note.—The University of California Publications are offered in exchange for the publications of learned societies and institutions, universities and libraries. Complete lists of all the publications of the University will be sent upon request. For sample copies, lists of publications or other information, address the Manager of the University Press, Berkeley, California, U. S. A. All matter sent in exchange should be addressed to The Exchange Department, University Library, Berkeley, California, U. S. A.

OTTO HARRASSOWITZ, LEIPZIG.

Agent for the series in American Archaeology and Ethnology, Classical Philology, Education, Modern Philology, Philosophy, Psychology, History.

R. FRIEDLAENDER & SOHN, BERLIN.

Agent for the series in American Archaeology and Ethnology, Botany, Geology, Geography, Mathematics, Pathology, Physiology, Zoology, and Memoirs.

ZOOLOGY.—W. E. Ritter and C. A. Kofoid, Editors. Price per volume, $3.50; beginning with vol. 11, $5.00.

This series contains the contributions from the Department of Zoology, from the Marine Laboratory of the Scripps Institution for Biological Research, at La Jolla, California, and from the California Museum of Vertebrate Zoology in Berkeley.

Cited as Univ. Calif. Publ. Zool.

Volume 1, 1902-1905, 317 pages, with 28 plates $3.50

Volume 2 (Contributions from the Laboratory of the Marine Biological Association of San Diego), 1904-1906, xvii + 382 pages, with 19 plates $3.50

Volume 3, 1906-1907, 383 pages, with 23 plates $3.50

Volume 4, 1907-1908, 400 pages, with 24 plates $3.50

Volume 5, 1908-1910, 440 pages, with 34 plates $3.50

Volume 6, 1908-1911, 478 pages, with 48 plates $3.50

Vol. 7. (Contributions from the Museum of Vertebrate Zoology.)

1. Two New Owls from Arizona, with Description of the Juvenal Plumage of *Strix occidentalis occidentalis* (Xantus), by Harry S. Swarth. Pp. 1-8. May, 1910 ..... .10
2. Birds and Mammals of the 1909 Alexander Alaska Expedition, by Harry S. Swarth. Pp. 9-172; plates 1-6; 3 text-figures. January, 1911. 1.50
3. An Apparent Hybrid in the Genus *Dendroica*, by Walter P. Taylor. Pp. 173-177. February, 1911 ..... .05
4. The Linnet of the Hawaiian Islands: a Problem in Speciation, by Joseph Grinnell. Pp. 179-195. February, 1911 ..... .15
5. The Modesto Song Sparrow, by Joseph Grinnell. Pp. 197-199. February, 1911 ..... .05
6. Two New Species of Marmots from Northwestern America, by H. S. Swarth. Pp. 201-204. February, 1911 ..... .05
7. Mammals of the Alexander Nevada Expedition of 1909, by Walter P. Taylor. Pp. 205-307. June, 1911 ..... 1.00
8. Description of a New Spotted Towhee from the Great Basin, by J. Grinnell. Pp. 309-311. August, 1911 ..... .05
9. Description of a New Hairy Woodpecker from Southeastern Alaska, by H. S. Swarth. Pp. 313-318. October, 1911 ..... .05
10. Field Notes on Amphibians, Reptiles and Birds of Northern Humboldt County, Nevada, with a Discussion of Some of the Faunal Features of the Region, by Walter P. Taylor. Pp. 319-436, plates 7-12. February, 1912 ..... 1.00

Index, pp. 437-446.

Vol. 8.

1. The Vertical Distribution of *Eucalanus elongatus* in the San Diego Region during 1909, by Calvin O. Esterly. Pp. 1-7. May, 1911 ..... .10
2. New and Rare Fishes from Southern California, by Edwin Chapin Starks and William M. Mann. Pp. 9-19, 2 text-figures. July, 1911. .10
3. Classification and Vertical Distribution of the Chaetognatha of the San Diego Region, Including Redescriptions of Some Doubtful Species of the Group, by Ellis L. Michael. Pp. 21-186, pls. 1-8. December, 1911. 1.75
4. Dinoflagellata of the San Diego Region, IV. The Genus *Gonyaulax*, with Notes on Its Skeletal Morphology and a Discussion of Its Generic and Specific Characters, by Charles Atwood Kofoid. Pp. 187-286, plates 9-17.

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY

Vol. 11, No. 15, pp. 511-528, pls. 25-26, 1 text fig. April 15, 1914

PARASYNAPTIC STAGES IN THE TESTIS OF *ANEIDES LUGUBRIS* (HALLOWELL)

BY

HARRY JAMES SNOOK AND J. A. LONG

Introduction

In many of the theories proposed to account for the segregation of hereditary factors a more or less specific association between the factors and the chromatic elements of the cell is assumed. Any judgment as to the tenability of such theories ought to be based, at least in part, upon the behavior of the chromosomes themselves, the phenomena of synapsis being particularly significant in this connection. The present study has been undertaken in an effort to obtain as much evidence as possible about the actual conditions during the synaptic period. Inquiries into the spermatogenesis of amphibians have contributed much towards a solution of the problem, and it has seemed worth while to extend the observations to another representative of the same class. An attempt has been made to answer the following questions: Is there a stage, or a series of stages, in spermatogenesis during which two or more chromosomes unite, or in any manner become very closely associated? If so, in what manner and to what extent does the process take place, and what is the subsequent fate of the elements which have been joined together? This inquiry is limited to the synaptic period and the stages which precede or immediately follow it.

The urodele, *Aneides* (= *Autodax*) *lugubris* (Hallowell), was chosen as the subject of this investigation for the following

Smithsonian Institution
MAY 6 1914
National Museum

reasons: (1) The male sex cells are large; (2) the animal is fairly common in this vicinity and may be obtained throughout the entire year; and (3) the seriation of stages within the testes is easily followed because all phases are frequently found in a single testis, beginning at the anterior end with lobules of spermatogonia and passing posteriorly to a region occupied by mature spermatozoa. Moreover, the cells in any particular lobule appear to have reached approximately the same stage in differentiation.

The material used for this research was obtained within a radius of five miles from Berkeley, with the exception of a few specimens from Twin Peaks, San Francisco, and much of it was secured upon the campus of the University of California. The salamanders may readily be found under stones and logs or in crevices of the rocks. They have also been taken in burrows at least a foot below the surface of the soil, but in all such cases observed the burrow opened beneath a rock. It is difficult to find them during the dry season, as they seek the deeper, moist levels. According to the investigations of Ritter and Miller (1899), they breed in June and July. Although no specimens were collected during June, July, and September, material was obtained during every other month.

A number of fixing fluids and staining processes were tried with varying success. Bouin's, Zenker's, and Flemming's fluids proved most valuable and were extensively employed. Gilson's fluid seemed to damage the cells of the outer cysts; otherwise, some very good late prophases were obtained by its use. The testes were embedded in paraffin and sectioned longitudinally in order to show the seriation to the best advantage. The sections, cut from six to twelve micra in thickness, were mounted on slides in the usual way.

With Bouin's and Zenker's fluids three stains were tried: iron-alum-haematoxylin with orange G and acid fuchsin as counterstains; safranin followed by gentian violet; and phosphotungstic acid haematoxylin. The last seems to be the best for general purposes, as it stains the growing spermatocyte beautifully without overstaining the mitotic figures. It differentiates the structures of the cell very clearly, staining the chromosomes deep blue and the spindles reddish. Many equatorial plates can

be excellently demonstrated with safranin and gentian violet after Zenker's or Bouin's solutions. Material fixed in Flemming's solution was stained either with safranin and gentian violet after the Gram method, or with iron-alum-haematoxylin and orange G. Gilson's fluid was followed by safranin and lightgreen.

A few testes, fixed in Flemming's solution and passed through the alcohols to seventy per cent, were divided into four or five parts which were transferred with a drop of alcohol to slides prepared with egg albumen and then thoroughly crushed and ground up under a cover glass. The seventy per cent alcohol was then drawn off and the albumen coagulated by dropping ninety per cent alcohol upon it, fixing the fragments and loose cells to the glass. The material thus prepared was carried through the alcohols and stained either in iron-alum-haematoxylin without counterstains, or in safranin with gentian violet. While many of the cells were broken up, or flattened out, a considerable number remained intact. Because of their large size they are somewhat opaque, but most of them are clear enough for study. This method destroys every evidence of seriation and for that reason is not of great value by itself, yet, taken in connection with the sectioned material, it has been found very useful. This type of preparation, in which the structures are entire, was most largely used in the determination of the number of chromosomes previous to the first maturation division.

The Spermatogonia

The anterior portion of the testis is occupied by spermatogonia and occasionally lobules may be seen which are filled entirely, or in part, with cells in the process of division. Among these it is possible to pick out polar views of the equatorial plate. By first carefully drawing them with the aid of a camera lucida, and then counting the chromosomes shown in the resulting sketch, the number and form were determined. It was not always possible to demonstrate each element clearly, owing to the sinuous form of many of the chromosomes and the tendency for them to gather in clumps, more or less masking those below; and in

many cases it could only be discerned that there were more than twenty-five and less than thirty. Discarding the latter as doubtful, there still remained nine clear cases in which the number was definitely twenty-eight, and one case, just as clear, in which it was only twenty-three.

Plate 25, figure 1, represents this latter and plate 25, figure 2, illustrates the more usual condition. They are drawn from cells in one section, located near each other in the same lobule. The two small elements in the center of the plate in both figures are quite characteristic of this stage, and, although they cannot always be found occupying the same relative position, and may sometimes be widely separated, they can usually be identified with chromosomes of the same general size and shape lying within the ring in other spindles. The chromosomes appear to be band-shaped and are usually bent into the form of a letter U with the free ends pointing outward. There is considerable variation in size and shape and in their position with reference to the spindle.

A split can frequently be discerned in the chromosomes of the equatorial plate, as is shown by several elements in the cells figured. It is believed that this is evidence that the plate is fully formed and that division is about to occur. Many dividing cells are situated in the immediate vicinity of these two.

The significance of the lesser number shown in figure 1 is not known, nor is it possible to say just how widely such variations occur. In the case under consideration there is no evidence that the condition is in any sense abnormal, for it does not differ from the others except in the number of chromosomes. This plate lies in a section twelve micra thick, and the following section shows only a few tips in the remainder of the cell.

Although such exceptional cases certainly exist, even a casual exploration of the lobules of dividing spermatogonia will convince one that in a large majority of cases more chromosomes are present than are delineated in figure 1. In view of the fact that in every clear case found, with the exception noted, twenty-eight definite elements could be made out, it seems justifiable to say that the number of chromosomes in the equatorial plate of *Aneides* is usually, but not universally, twenty-eight.

The Spermatocyte

Following the last spermatogonial telophase, the chromatin becomes very diffuse and is irregularly distributed in the form of clumps or "net-knots" connected by fine threads (pl. 25, fig. 3). If there is any arrangement or order in these threads, it is completely masked by the patches of chromatin, nor is there any suggestion of orderliness in the size or distribution of the latter. There is no clear evidence of a "chromoplast" as described by Eisen (1900) and later by Janssens (1905) in the male sex cells of *Batrachoseps attenuatus*.

Janssens also found evidence of a rotation of the nucleus during this period, whereby the "chromoplast," at first in the neighborhood of the sphere, came to lie opposite it. In *Aneides* the sphere is found at one side of the nucleus, but further than that it has been impossible to demonstrate any relation between it and the elements of the nucleus until the resting stage is past.

In lobules more posterior than those containing the resting nuclei the fine threads gradually become more pronounced and can be followed without difficulty for considerable distances. At the same time it is plain that the threads are of greater diameter and stain more heavily in the region of the sphere than in the rest of the nucleus. The net-knots appear smaller and are comparatively few, especially in the immediate vicinity of the sphere, which may be said to lie at the proximal pole of the nucleus. In this region the threads appear somewhat condensed (pl. 25, fig. 4) and close observation shows that they are associated two by two in such a manner that when viewed from the side they resemble the letter V, with the angle pointing toward the sphere and the diverging arms prolonged in the opposite direction. They are unbranched, as was also found to be true for *Salamandra* by the Schreiners (1906) and for *Batrachoseps* by Janssens (1905), the description of the conditions in *Batrachoseps* being confirmed by Wilson (1912), who examined Janssens' preparations. Sections fixed in Bouin's, Zenker's, or Flemming's solutions and stained in a variety of ways show this peculiarity. At this stage the distal portion of the nucleus shows no such polar orientation, and if the sections should be so cut

as to include this part only it could be distinguished with extreme difficulty, if at all, from the preceding stage.

Comparatively few of the cells examined exhibited the V-figures when observed from the side, the greater number displaying a Y-shaped arrangement of the threads in the vicinity of the proximal pole, with the stem of the Y ending in the immediate neighborhood of the sphere and the arms drawn out into fine threads which are lost in the distal portion of the nucleus (pl. 25, fig. 5). In the part of a section which contains spermatocytes in this condition there is a gradual change from the V- to the Y-figure; the cells characterized by the short-stemmed Y-figures give place gradually to those in which a long-stemmed figure predominates (pl. 25, figs. 6 and 7); and in the individual nuclei there is considerable variation in the length of the structure from the free end to the fork. At times the thick threads seem also to be double, but it is not possible to demonstrate this condition in most cases. As the length of the stems of the Ys increases the extent of the network diminishes.

As can be easily imagined, it is practically impossible to determine with accuracy in this stage the number of the V- and Y-figures, and of the fine threads of which they are composed. While the threads are perfectly clear in side views, they are easily confused when seen from one end. Nevertheless, in one nucleus corresponding to figure 4, so cut that the part containing the pairing threads was viewed from the pole, a diagram indicated the presence of twenty-six to thirty Vs and Ys, or, in other words, of fifty-two to sixty threads; and in another case in a stage like that shown in figure 6 there were clearly twenty-eight thick threads (stems of Ys).

This stage corresponds closely to that figured by Janssens (1905) in his paper on the spermatogenesis of *Batrachoseps* and designated by him the amphitene, in distinction to the preceding or leptotene condition in which the fine threads are not united. Much stress is placed upon it by the Schreiners (1906) in their discussion of the spermatogenesis of *Salamandra maculosa* as the stage in which a conjugation of the chromosomes takes place. Many writers have overlooked it entirely, because, no doubt, of its close resemblance to the leptotene period and the small number

of nuclei usually found in this condition. If the number of amphitene cells can be taken as an indication of the duration of the period, it must be considered as relatively short, because the cells occupy a much smaller proportion of the testis than either the spermatogonia or the cells that have advanced to the next stage.

Posterior to the region in the testis last described are nuclei containing horseshoe-shaped loops, with their free ends turned towards the sphere and their bends in the distal half. They appear somewhat granular (pl. 25, fig. 8 and pl. 26, fig. 10). These loops have been described in a number of urodeles and would appear to be very characteristic of spermatogenesis in salamanders. In thickness they exceed somewhat the thick threads formed by the union of two fine diverging ones. No trace of the latter can now be seen. Cross-sections through the proximal portion of the nucleus show clearly twenty-eight cut ends, demonstrating the number of loops to be fourteen (pl. 26, fig. 11). Polar views show the presence of twenty-eight converging threads with their free ends crowded together in the immediate vicinity of the sphere and very near to the nuclear membrane (pl. 26, fig. 9).

It will be remembered that this polar orientation is also a characteristic of the preceding stage, a lateral view showing the same arrangement of the thick threads forming the stem of the Y-figure as is here presented by the ends of the loops. This resemblance is very marked, indeed, and together with the evidence afforded by seriation leads to the conclusion that the loop is derived from two fine threads which have now completely disappeared as separate threads and have fused into one.

Up to this point the cells have been gradually increasing in volume, a fact which makes seriation more certain; but during the stage of well-developed loops relatively little growth takes place. As the cells in this condition usually occupy a rather large portion of the testis, it seems probable that this period lasts for a much longer time than the amphitene stage.

Later all evidences of polarization are lost and the chromosomes end without apparent relation to the position of the centrosomes or to each other. At the same time a longitudinal split develops, dividing each loop more or less completely into two

portions throughout the greater part of its length, but leaving one or both of the ends intact (pl. 26, fig. 12), a process which is the reverse of the one previously described. Cells in which the split is developing can readily be distinguished from those in the amphitene stage, by the absence of polarization, by their larger size, and by their position in the testes near the region in which the maturation divisions take place. They are separated from the amphitene cells by the extensive and clearly defined region of the polarized loops.

This and the subsequent stages in amphibians have been described so frequently since first pointed out by Fleming (1887) that they need not be discussed in detail here. According to Hermann (1889), Meves (1897), Eisen (1902), Janssens (1901, 1905), Kingsbury (1902), and other careful investigators, the longitudinal halves of the loop are separated in the first maturation division. This seems to be true in the case of *Ancides*. The split loops shorten, thicken, and at the same time become twisted to form what Janssens designates the streptotene stage (pl. 26, fig. 13). They finally form heterotypical chromosomes, the halves of which, corresponding to the halves of the split loops, pass to opposite poles during the following anaphase.

A number of spindles representing the first maturation division were examined and some drawn with the aid of the camera lucida (pl. 26, fig. 14). The number of chromosomes was fourteen, though fifteen were counted in two cases. In the latter, however, from the position of the chromosomes it seems probable that a chromosome had just divided and it is possible that fourteen was the original number in all cases examined. Both sections and entire cells were employed in making these counts, the latter being found particularly valuable. While they are frequently somewhat dense and often pressed out of shape, it is hardly possible that any of the chromosomes could be lost without rupturing the cell membrane. In that case the loss would be detected.

Discussion and Conclusions

As previously mentioned, the usual number of chromosomes found in the equatorial plate of the spermatogonial spindle is

twenty-eight. In the stage of the polarized loops, cross-sections and polar views in the neighborhood of the sphere indicate the number of loops to be fourteen, which agrees with the number of chromosomes comprising the equatorial plate of the first maturation division. This difference between twenty-eight and fourteen is to be expected if the chromosomes conjugate whether by the parasynaptic or telosynaptic method.

Meves (1911) avoids the problem of synapsis by stating: "Die Geschlechtszellen bezw. ihre Kerne haben nach meiner Vorstellung (1907) die besondere Eigenschaft ererbt, beim Eintritt in die Wachstumsperiode nur die halbe Zahl von Chromosomen auszubilden." To which Wilson (1912) replies, "Certainly the adoption of this simple solution would save a great deal of trouble; but I fear that the facts compel us to take a more roundabout way out of our difficulties." A condition so well-defined and clear as the amphitene stage would seem to be too significant to be thus lightly considered.

This has been interpreted by different investigators to represent either a union of two threads (the Schreiners (1906), Janssens (1905, 1908), Wilson (1911), or a splitting of one Meves (1908), Goldschmidt (1908), Fick (1908). In *Aneides* the evidence afforded by seriation as recapitulated below seems to the writers to point toward the former interpretation.

1. Fine, unpaired threads become polarized with respect to that side of the nucleus near which lies the sphere, the proximal pole.

2. Coincident with this polarization, threads are found associated two by two at the proximal pole of the nucleus.

3. By the association of any two threads there is formed a figure, which, when observed from a position at right angles to an axis passing through the poles of the cell, resembles the letter V with the angle turned toward the sphere.

4. Seriation shows that the V-shaped figures are succeeded by Y-like figures, of which the stem, frequently exhibiting a double condition, lies in the region of the centrosomes, while the arms diverge widely away from the sphere. Furthermore, it may be observed that as this stage becomes more advanced, the stem of the Y increases in length at the expense of the arms.

5. More posterior in the testes the Y-figures are replaced by loops showing the same polarization, i.e., with the free ends directed toward the sphere while the bends are found in the region opposite to the centrosomes.

6. At this stage the fine threads can no longer be detected and the loops appear as single threads.

This evidence leads to the conclusion that the loops are formed by the union of the fine threads. A more critical examination of the early stages raises the question as to what are the relations of the conjugating leptotene threads to each other. Up to this point the individual V- or Y-figures described in any one nucleus have been considered as unrelated to each other. If there are only fourteen bifid figures in any one nucleus, each must be considered one end of a loop in the later polarized stage, the other end of the loop not yet having come into existence. But since there are about twenty-eight pairs of threads at the beginning of polarization and since the twenty-eight free ends of the completed loops directed toward the proximal pole correspond in position to the stems of the Ys, it leads one to think that the two ends of each loop are formed simultaneously and before the middle part comes into existence.

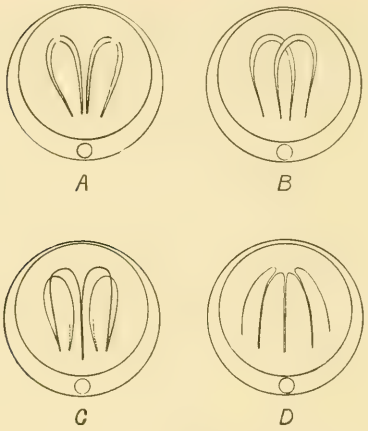
While the foregoing is strong evidence that the stem of each Y-figure becomes one end of a polarized loop, the way in which the two ends of each loop become associated remains to be considered. It will be remembered that each one of the fifty-six short, fine, leptotene threads which unite in one way or another to form the fourteen loops is indirectly continuous with the others through the medium of the network. The further evolution of these threads might be thought of in one of two ways. In the first place the fifty-six threads might be imagined as separate, individual filaments which pair to form the twenty-eight Y-figures; in the second place, they may be conceived of as not so many independent parts, but as so definitely related that each branch of each Y would be one end of a potential thread, the other end of which would be represented by one of the branches of some other Y.

In regard to the first of these possibilities, it might be argued that the arms of the Y-figures on one side meet and join with

similar arms of Y's on the other side, giving rise to the loop by a process of telosynapsis in addition to parasynapsis (fig. *A*). That there is no evidence for such a conclusion is indicated by the observation that threads may frequently be followed for long distances around the nucleus and that free ends have never been found except in the vicinity of the sphere. When the threads are definitely formed, there are no morphological indications that an end-to-end union has taken place.

These considerations indicate at once the validity of the second alternative, for if the threads exhibit no free ends except at the proximal pole of the nucleus, where they unite to form the Y-figures, it seems reasonable to conclude that they represent the ends of twenty-eight threads which are evolved from their ends towards their middle at the expense of the nuclear network. In other words, each of the fifty-six threads becomes directly continuous with one only of its own kind by the time that the loops are complete. If this conception of their origin and nature be sound, the way in which they become associated in the loops might be interpreted in one of two ways: (1) The loops may be formed by the association of two potential threads by a process which begins at approximately the same time at both ends (fig. *B*). (2) One leptotene thread might be joined at the ends to two other threads (fig. *C*). Both of these interpretations have one feature in common, that of a side-to-side union. There seems, however, to be little reason to believe that the second condition actually exists in the male sex cells of *Ancides*. If each leptotene thread were joined at the ends to other threads at the beginning of polarization (fig. *C*), as the bifid figures closed up, most of the threads would be drawn together in one or more points in the region of the distal pole of the nucleus (fig. *D*), which is, in fact, the region of widest separation. The fact that there is no evidence of such behavior upon the part of the threads would seem to dispose of this interpretation.

Therefore, it seems probable that the number of pairing threads is twenty-eight and that, as rapidly as they are evolved, they unite two by two, side by side, and at both ends, the middle part of the potential threads being lost in the distal half of the nucleus.



Figs. *A* to *D*.—Diagrams to illustrate possible modes of association in synapsis of the fifty-six fine threads (leptotene) which are formed from the nuclear network and become polarized with regard to the sphere which lies at the proximal side of the nucleus. The large outer circle represents the cell wall; the large inner, the nuclear membrane; the small one between the two large, the sphere.

Fig. *A*.—Of the fifty-six threads which are imagined as separate, distinct filaments eight are represented as forming two loops (amphitene) by a double process of pairing. They form by parallel union four (of the twenty-eight) Ys which by end to end junction give rise to the loops. There is no evidence of such a condition.

Fig. *B*.—Four complete threads are indicated, the eight ends of which, corresponding to the eight separate threads of figure *A*, arise separately, are at first merged into the nuclear network of the distal part of the nucleus, and with the disappearance of the network become continuous as four threads. These before completion and while potentially present in the network become paired in such a manner that the ends of two threads unite to form two Ys, which by closing up give rise to a single loop which is unconnected with the other. Fourteen such loops are formed.

Fig. *C*.—The complete threads arise as in figure *B*. A different mode of synapsis is represented in which the two ends of one complete thread are not paired with the two ends of only *one* other thread, but with one end each of *two* other threads.

Fig. *D*.—A later stage of the condition shown in figure *C*, showing how with the final closing of the Ys the bends of the loops would be drawn together, a condition not existing.

With these facts and considerations in mind, it is concluded that the V- and Y-figures do not indicate a splitting, as maintained by some, but that they represent a progressive, parallel union or conjugation of fine (leptotene) threads; in other words, a parasynaptic union. This union takes place during the amphitene stage and leads to the formation of the single, thick, polarized loops. There is no reason for confusing the split which does occur in the stage following the formation of the loops (and which may be the reverse of parasynapsis) with the union in the amphitene stage, since the two stages are easily distinguishable both by their appearance and position in the testis.

The evidence set forth above does not warrant an assertion that the conjugating leptotene threads are identical with the spermatogonial chromosomes. Nevertheless, the fact that the number of chromosomes (tetrads) in the first maturation spindle is half that of the chromosomes in the spermatogonial division, together with the evidence that the tetrads are formed by the union of threads evolved from the nuclear network which in turn is formed from the chromosomes of the last spermatogonial telophase, suggests very strongly that the spermatogonial chromosomes which went into the nuclear network reappear as the pairing leptotene threads. This idea is further supported by the manner in which the two branches of two Ys become continuous as though they were the ends of threads (chromosomes) potentially existing in the network, though not distinguishable as such. Or, to reverse the conception, if it is considered that the spermatogonial chromosomes retain their continuity throughout the resting stage of the nucleus, then it is easier to comprehend why the proper Y-figures become associated as the leptotene threads are evolved, for the chromosomes, though in modified form and only partly distinguishable as threads, begin to pair as they might if pairing were delayed until they were completely formed. Although this way of stating the conception is open to the criticism that it is an argument in a circle, still the conception is worthy of consideration as having some weight on the positive side of the question of the individuality of the chromosomes.

It has already been pointed out that the stage of the polarized loops which follows that of the conjugation of the leptotene

threads has a relatively much longer duration than any other of the stages of the prophase of the first maturation division. If it is true that the conjugating threads have the value of paired maternal and paternal chromosomes and constitute the mechanism for the segregation and recombination of mendelian characters or their factors, it is to be noted that there is ample opportunity for the reconstitution of the chromosomes and for any interchange of substances composing the chromosomes which may be concerned in the transmission of inherited characters.

Summary

1. The usual number of chromosomes found in the spermatogonia of *Aneides lugubris* is twenty-eight.

2. The V-figures at the beginning of polarization number twenty-six to thirty, and Ys at a slightly later stage twenty-eight.

3. The number of polarized loops and of tetrads formed from the loops is fourteen.

4. Each tetrad is the result of a parasynaptic union of fine threads.

Transmitted May 3, 1913.

LITERATURE CITED

Eisen, G.
1900. The spermatogenesis of *Batrachoseps*. Journ. Morph., **17**, 1–117, pls. 1–14, 12 figs. in text.

Fick, R.
1908. Zur Konjugation der Chromosomen. Arch. f. Zellforsch., **1**, 604–611.

Flemming, W.
1887. Neue Beiträge zur Kenntnis der Zelle. Arch. f. mikr. Anat., **29**, 389–463, pls. 23–26.

Goldschmidt, R.
1906. Review of work of the Schreiners. Zool. Centralblatt, **13** 611–612.
1908. Ist eine parallele Chromosomen-konjugation bewiesen? Arch. f. Zellforsch, **1**, 620–622.

Janssens, F. A.
1901. La spermatogénèse chez les tritons. La Cellule, **19**, 7–116, 3 pls.
1905. Evolution des auxocytes mâles du *Batrachoseps attenuatus*. *Ibid.*, **22**, 377–425, 7 pls.

Janssens, F. A. et Dumez, R.
1903. L'élément nucléinien pendant les cinèses de maturation des spermatocytes chez *Batrachoseps attenuatus* et *Plethodon cinereus*. La Cellule, **20**, 419–461, 5 pls.

Janssens, F. A. et Willems.
1908. Spermatogénèse dans les batraciens, IV. Le spermatogénèse dans l'*Alytes obstetricus*. La Cellule, **25**, 151–173, 2 pls.

Kingsbury, B. F.
1902. The spermatogenesis of *Desmognathus fusca*. Amer. Journ. Anat., **1**, 99–135, pls. 1–4, 1 fig. in text.

McGregor, J. H.
1899. The spermatogenesis of *Amphiuma*. Journ Morph., **15** (Supplement), 57–104, pls. 4–5.

Meves, F.
1896. Ueber die Entwicklung der männlichen Geschlechtzellen von *Salamandra maculosa*. Arch. f. mikr. Anat., **48**, 1–83, pls. 1–5.
1908. Es gibt keine parallele Konjugation der Chromosomen. Arch. f. Zellforsch., **1**, 612–619, 1 fig. in text.
1911. Chromosomenlangen bei Salamandra, nebst Bemerkung zur Individualitätstheorie der Chromosomen. Arch. f. mikr. Anat., **77**, Abt. 2, 273–300, pls. 11–12.

Montgomery, T. H.
1903. The heterotypic maturation mitosis in Amphibia and its general significance. Biol. Bull., **4**, 259–269, 8 figs. in text.
1904. Some observations and considerations upon the maturation phenomena of the germ cells. *Ibid.*, **6**, 137–158, 30 figs.
1911. The spermatogenesis of an hemipteron, *Euchistus*. Journ. Morph., **22**, 731–798, 5 pls.

Ritter, W. E., and Miller, L.
1899. A contribution to the life-history of *Autodax lugubris* Hallow, a California salamander. Amer. Nat., **33**, 691–704, 7 figs. in text.

Schreiner, A. und K. E.
1906 a. Neue Studien über die Chromatinreifung der Geschlechtszellen; I. Die Reifung der männlichen Geschlechtszellen von *Tomopteris onisciformis*. Arch. Biol., **22**, 1–69, pls. 1–3, 2 figs. in text.
1906 b. II. Reifung der männlichen Geschlechtszellen von *Salamandra maculosa* (Laur.), *Spinax niger* (Bonap.) und *Myxine glutinosa* (L.). *Ibid.*, **22**, 419–492, pls. 23–26, 1 fig. in text.

Wilson, E. B.
1912. Studies on chromosomes, VIII. Observations on the maturation-phenomena in certain Hemiptera and other forms, with considerations on synapsis and reduction. Journ. Exp. Zool., **13**, 345–431, 9 pls.

PLATE 25

All the figures are drawn at the same magnification (x 2350) with a Spencer 2 mm. objective, a Zeiss No. 12 compensating ocular, and an Abbe camera lucida. Reduced magnification on plates, 1700 diameters.

Fig. 1. Spermatogonium in the equatorial plate stage, showing twenty-three chromosomes. Fixed in Zenker's fluid and stained with iron-alum haematoxylin and orange G.

Fig. 2. Same stage as above but with the usual number of chromosomes (twenty-eight). Zenker's fluid, iron-alum haematoxylin, and orange G.

Fig. 3. Spermatocyte before the beginning of polarization. Fixed in Zenker's solution and stained with phosphotungstic acid haematoxylin.

Fig. 4. Spermatocyte at the beginning of polarization showing V-figures. Zenker's fluid and phosphotungstic acid haematoxylin.

Fig. 5. Spermatocyte with short-stemmed Y-figures. Phosphotungstic acid after Zenker's fluid.

Figs. 6 and 7 illustrate successive steps in the pairing of the threads. The section from which Fig. 6 was taken was fixed in Zenker's solution and stained with phosphotungstic acid haematoxylin. Figure 7 was taken from material fixed in Bouin's fluid and stained with iron-alum haematoxylin.

Fig. 8. A lateral view. Loops completed. Zenker's fluid and phosphotungstic acid haematoxylin.

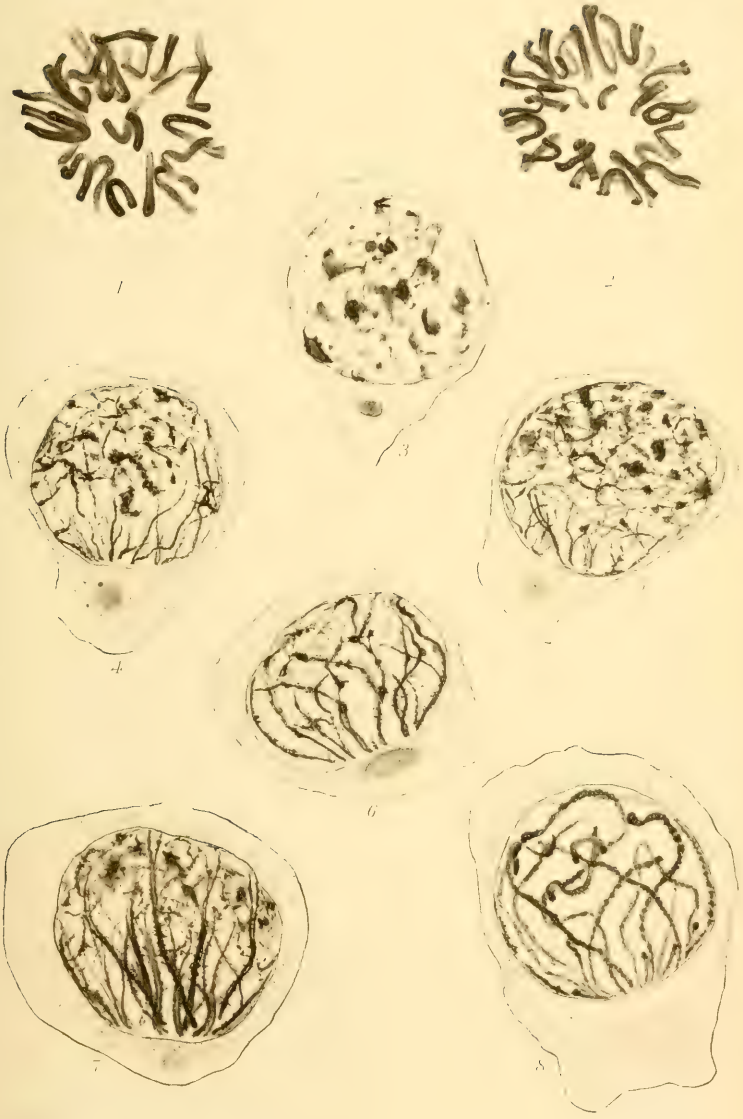


PLATE 26

Fig. 9, 10, and 11. The loops completed.

Fig. 9. Pole view. The sphere lies above the nucleus. The twenty-eight free ends in the vicinity of the sphere represent fourteen loops. Zenker's fluid and phosphotungstic acid haematoxylin.

Fig. 10. Lateral view. Zenker's fluid, iron-alum haematoxylin, and orange G.

Fig. 11. Section of spermatocyte in the loop stage. The loops are cut twice. Fixed in Zenker's fluid and stained with iron-alum haematoxylin.

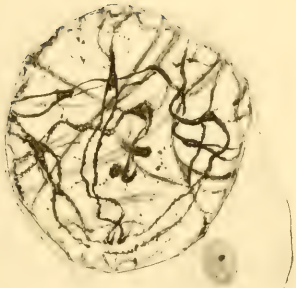
Fig. 12. Complete cell from crushed preparation showing the beginning of the split. Flemming's fluid and iron-alum haematoxylin.

Fig. 13. "Strepsinema." Only a small portion of the cell included in the section. Gilson's fluid, iron-alum haematoxylin, and orange G.

Fig. 14. Prophase to first maturation division. Complete cell from crushed preparation—somewhat flattened. Flemming's fluid and iron-alum haematoxylin.

9

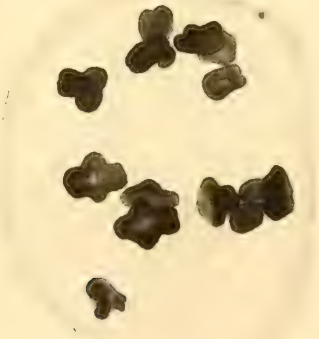
10



12

11

13



14

INDEX*

Acclimatization of leeches, to repeated jars, 261; to successive shadows, 263; causative factors of, 265.
Accipitres, 331.
Acridiidae, 429.
Acridiinae, 429.
Adams, G. P., cited, 227.
Aftershafts, of down feathers, 332; of wing coverts, 346, 347.
Agalenidae, food of meadowlark, 435.
Agassiz, Alexander, 307.
Agassiz, L., 316.
Agelaius phoeniceus californicus, 5, 6, 18.
  tricolor, 6, 19.
Albinism, in meadowlarks, 492.
Allobophora foetida, 216.
Alula, 348, 364; barbs, 349; barbules, proximal distal, 349.
Alydus, 483.
Amitotic division, 167, 169.
Ammothea alaskensis, 132, 137.
  gracilipes, 132.
  latifrons, 132.
  nudiuscula, 132; description, 135; measurements, 137.
  pribilofensis, 132.
Ammothella, bi-unguiculata var. californica, 127, 130, 132; measurements, 130.
  spinosissima, 130, 132; measurements, 130.
  tuberculata, 132.
Amphibian Larvae, Control of Pigment Formation in, 53.
Amphidinium, 27.
Amphitene stage in spermatogenesis, 516.
Anasa, food of meadowlark, 432.
Aneides lugubris, parasynapsis in, 511.
Anoplodactylus californicus, 129, 133.
  erectus, 133.
Antibody, specific, 46.
Ants, food for meadowlark, 433.
Apidae, 434.
Aphis brassicae, 432.
  mellifera, food for meadowlark, 433.
Ardea herodias herodias, 5.
Arietellus **pacificus**, 189.
Arthropods, 492; protective adaptations of, 492.
Astragalinus psaltria hesperophilus, 5.
Astur, 331.
Augaptilus **californicus**, 186.
  depressus, 187.
  romanus, 188.
  simplex, 188.
Aughey, Samuel, 1, 6.
Availability, definition of, 492.
Ballowitz, E., cited, 144.
Barbicels, pl. 17, opp. p. 370; pl. 18, opp. p. 372; pl. 19, opp. p. 374.
Barbs, of down feathers, 332; of oil-gland feathers, 334; of filoplumes, 335; of remiges, 337, 340; of wing coverts, 345, 346; of rectrices, 350; of contour feathers of trunk, 352. *See also* Alula.
Barbules, of down feathers, 333; of oil-gland feathers, 334; of filoplumes, 335; of remiges, 340; proximal, of wing coverts, 341, 342, 344, 346, pl. 17, opp. 370, pl. 18, opp. p. 372, pl. 19, opp. p. 374; proximal, of humerals, 347; of rectrices, 350; of contour feathers, 353; distal, of wing coverts, 341, 343, 344, 346; of rectrices, 350; of contour feathers of trunk, 352–357.
Bees, 483; food for meadowlark, 433.
Beetles, food of meadowlark, 426.
Behavior of Leeches, The, With Especial Reference to Its Modifiability. A. The General Reactions of the Leeches *Dina Microstoma* **Moore and** *Glossiphonia Stagnalis* **Linnaeus. B. Modifiability in the Behavior of the Leech** *Dina Microstoma* **Moore**, 197.
Behavior of young leeches. *See* Leech behavior.

* Univ. Calif. Publ. Zool., vol. 11.

Bibliography, 20, 28, 49, 84, 125, 150, 169, 179, 301, 366, 494, 524.
Biedermann, W., cited, 143.
Birds in Relation to a Grasshopper Outbreak in California, 1.
Birds, time of digestion, 7; insect remains in feces of, 7; stomach examinations, 9; stomach contents, 10; economic value of, 13; insectivorous, 15; damage caused by, 19; economic relations of, 379; feeding habits, 2; relations to insects, 2, 49; captive birds, experimentation on, 491; censuses of, 4–6, 403, 409; game, 477; non-game, 477.
Bird plumage, 330.
Blackbird, 7, 19.
  Brewer, 5, 6, 8, 11, 18, 380, 457, 461.
  red-winged, 5, 6, 10, 13. *See* Red-wing, bicolored.
  yellow-headed, 6.
Blood-leech, its use in medical practice, 191.
Bluebird, western, 6.
Bohn, G., cited, 205, 251.
Bolsius, H., cited, 206.
Bombidae, 434.
Bombus californicus, food for meadowlark, 433.
Bougainvillia, 321.
Brain, its function in leeches, 248.
Bristles, 365; post-orbital, 359; supra-orbital, 359, pl. 20, opp. p. 376; loral, 360; rictal, 360.
Bryant, Harold C., 1, 377.
Bugs, food of meadowlark, 432.
Bunting, lazuli, 5.
Buprestidae, 427.
Butcherbirds, 7, 11.
Buteo, 336.
  swainsoni, 6.
Butorides virescens anthonyi, 5, 19.
Butterflies, food for meadowlark, 430, 431, 457, 459; self-protective characters of, 481, 482.
Calamus, of down feathers, 332; of remiges, 336; of greater upper wing coverts, 344; of greater under wing coverts, 345; of contour feathers of trunk, 352.
Calandridae, 427.
California State Fish and Game Commission, 1, 380.
Calkins, G. N., cited, 36.
Camnula pellucida, 3–4.
Camponotus, food for meadowlark, 433.
Captive birds, experiments on, 409.
Carabidae, 427, 428.
Carbon dioxide as a fatigue substance, 282.
Carpodacus mexicanus frontalis, 5, 379.
Carrel, 159.
Castle, W. E., cited, 55, 56, 218, 220, 234.
Catablema, 317.
Caterpillars, food of meadowlark, 431; protective characteristics of, 483.
Cell inclusions, 36, 38.
Cell parasites, protozoan, 39.
Centipedes, 436.
Chamberlain, F. M., 173.
Chandler, Asa C., 329.
Chat, long-tailed, 5.
Chemotactic responses in *Dina microstoma*, 229.
Chloretone, as a depressant on leeches, 279.
Chondestes grammacus strigatus, 5, 6.
Chromatophores, 143, 145, 147; effect of food on, 80.
Chromosomes, spermatogonial, of *Aneides lugubris*, 513, 523, 524.
Chrysis, food for meadowlark, 433.
Chrysotis festiva, 64.
Chrysididae, 434.
Chrysomelidae, 427, 428.
Chun, C., cited, 317.
Cicadidae, food for meadowlark, 432.
Cincindelidae, 427.
Circus aeruginosus, 331.
  cinerarius, 331.
  (cinereaceus?)
  hudsonius, feathers, 329–376; moults, 331; down feathers, 332; filoplumes, 334; remiges, 336, 363; macroscopic structure, 336; microscopic structure, 340; wing coverts, 344; alula, 348; rectrices, 350; contour feathers of trunk, 352; modified feathers of head, 357; conclusions,, 361; oil gland 362.
  pygargus (=cyaneus?), 331.
Clepsine plana, 202.
Clotenia occidentalis, 132.
Codonium princeps, 321.

Colaptes cafer collaris, 5.
Cole, Dr. Leon J., acknowledgment of assistance, 128.
Coleoptera, food of meadowlark, 426.
Collections, formation of, among leeches, 216; effect on, of lowering of temperature, 216; influence on, of light, 217; effect upon, of contact, 217.
Conozoa behrens, 4.
Conservation of wild life, 383.
Control, The, of Pigment Formation in Amphibian Larvae, 53.
Contour feathers of trunk, 352, 356. *See also* Feathers.
Copepoda of the San Diego Region, Fourth Taxonomic Report on, 181.
Coreidae, food for meadowlark, 432.
Corimelaena, 432.
Corymopsis, 321.
Coryzus, 483.
Councilman, T. W., 36.
Coverts, ear, 358, 365.
Coverts, tail, upper, 354; under, 356.
Coverts, wing. *See* Wing coverts.
Crickets, 11.
Crustacean, in food of meadowlark, 436.
Curculionidae, 427.
Curlew, 6.
Cushny, A. R., cited, 272, 273, 274, 278.
Cutworms, food of meadowlark, 431.
Cyanocitta stelleri frontalis, 457.
Cytorcyres variolae, 36.
Darwin, C., cited, 64.
Decapitation, effect of, on behavior of *Dina microstoma*, 245.
Dermestidae, 427.
Desiccation, ability to withstand, in *Dina microstoma* and *Glossiphonia stagnalis*, 232.
Diabrotica soror, 428, 485.
Diemyctylus, pl. 5, opp. p. 152, pl. 6, opp. p. 154, 158, 159.
torosus, 148.
Digestion, in birds, time of, 7.
Dina microstoma, description and distribution of, 206–207; feeding reactions, 219; starvation experiments on, 220; phototaxis in, 223; determining factors of the different response to the same stimulus, 256; *see also* Stimulation of *Dina microstoma;* fatigue from repeated contact stimuli, 267; directive influence of light on movements of, 225; chemotactic responses in, 229; tendency to geotactic response, 231; effect of decapitation on behavior of, 245; influence on, of strychnine, 273.
Dinosphaera, 22.
palustris, plates of, 21; description of, 23; figures of, 24, 25; skeleton of, 26; relationships, 27.
Dinosphaera palustris **(Lemm.), On the Structure and Relationships of**, 21.
Diptera, food for meadowlark, 434.
Directive influence of light on movements of *Dina microstoma* and *Glossiphonia stagnalis*, 225.
Dove, western mourning, 5, 380.
Down feathers, 332. *See also* Feathers *and* Powder-down.
Downy structure, 363.
Ducks, 12, 13.
Dytiscidae, 427.
Ear coverts, 358, 365.
Economic ornithology, a study in, 1, 377, 381, 388, 389; history of methods of, 389, 394; comparison of methods of, 397; problems of, 488, 493.
Eggshells, food of meadowlark, 437.
Ehrmann, cited, 143.
Elanoides, 331.
Elanus, 331.
Elateridae, 427, 428.
Eloedes, 428, 483.
Epithelioma Contagiosum of the Common Fowl, A Study of, 29.
Epithelioma contagiosum, economic importance, 29; scientific importance, 30; history, 31; clinical features, 32; period of incubation, 32; intravenous inoculation, 34; mucous membrane inoculation, 34; relationship of virulence of virus to resistance of host, 34; mildness of inoculated disease, 35; epidemiology, 35; pathology, 36; methods in study, 36; tissue reaction, 37; cell inclusion, 36, 38; form and occurrence in cells, 38; nature of inclusion, 39; changes in in-

clusions, 39; early immunity, 40; specific immunity, 41; relationship to roup, 41; development of roup in immune fowls, 42; possibility of double inoculation, 42; complement fixation, 43, 45; technique of bleeding fowls, 43, 45; appearance of specific antibody, 46.

Epithelium, Ectodermic, Behavior of in Tadpoles, When Cultivated in Plasma, 155.

Eristalis, food in meadowlark, 434.

Erotylidae, 427.

Esterly, C. O., 181.

Euchaeta **elongata**, 183.

Eugonia californica, 457.

Euphagus cyanocephalus, 5, 6, 18, 457.

Euphausia pacifica, 174.

Euschistus, 483.

Euvanessa antiopa, 483.

Eyelashes of *Circus hudsonius*, 359, 365.

Eye-spot. *See* ocellus.

Faeces of birds, insect remains in, 7; of meadowlark, 437.

Falco sparverius, 336.
sparverius, 6.

Fatigue in leeches, causes producing, 284.

Fatigue substances in leeches, 282; carbon dioxide, 282; monopotassium phosphate, 283; lactic acid, 284.

Feathers of *Circus hudsonius*, 329-376.

Feathers, contour, 363, 365; of the trunk, 352, 356; from the middle of the back, calamus, shaft, vanes, barbs, 352; distal barbule, proximal barbules, feathers of the upper back, of the nape, 353; of the crown, upper tail coverts, 354; under parts, lower breast, upper breast, 354; flanks, lower belly, legs, 355; under tail coverts, filoplumes, 356.
down, 332; calamus aftershafts, quill, 332; barbs, 332, 334; barbules, 333, 334; powder-down, 333; oil gland, 334; downy structure, in remiges and rectrices, 363.
modified, of the head, 357; facial ruff, 357; ear coverts, 358; post-orbital bristles, 359; supra-orbital bristles, 359; eyelashes, 359; loral bristles, 360; rictal bristles, 360.

Feathers, tail, 361, 365; of rectrices, 350.

Feathers, thumb. *See* Alula.

Feces of birds, insect remains in, 7; of meadowlark, 437.

Feeding reactions, analysis of, in leeches *Dina microstoma* and *Glossiphonia stagnalis*, 219.

Ficalbi, E., cited, 143.

Filoplumes of *Circus hudsonius*, 332, 334, 356, 360, 362; pl. 16, opp. p. 368.

Fisheries, relation of leeches to, 203.

Flicker, red-shafted, 5.

Flies, food of meadowlark, 434.

Food, effect of, on chromatophores, 80.

Formica, food of meadowlark, 433.

Formicidae, 434.

Franz, V., cited, 144.

Fucus, 129.

Fulgoridae, 429.

Fundulus, 144.

Gaetanus **ascendens**, 182.

Galovine, E., cited, 143.

Game birds, 477; non-game, 477.

Gaupp, cited, 143.

Gee, Wilson, 197; cited, 267.

Geotactic response, tendency to, in *Dina microstoma*, 231.

Gibbs, H., cited, 203.

Glossiphonia bioculata, 206.
complanata, 218.
heteroclita, 206.
sexoculata, 206.
stagnalis, description and distribution, 207; feeding reactions, 219; phototaxis in, 223; directive influence of light on movements of, 225; mode of fecundation, 234; experiments on "parental instinct," 235-240.
tessulata, 201.

Glushkiewitsch, T. H., cited, 245, 246.

Gobius, 144.

Goldfinch, green-backed, 5, 6.

Gonyaulax, 21, 22.
palustris, 21, 23.

Gortner, R. A., cited, 57, 58.

Grain seeds, destroyed by meadowlark, 442.

Grasshopper Outbreak in California, Birds in Relation to, 1.
Grasshoppers, 2, 3, 4, 18, 19, 429, 459.
Gravity, reactions to, in leeches, 230.
Grinnell, J., 18, 380.
Grosbeak, western blue, 5.
Gryllidae, 429.
Gryllus, 11, 429.
Guiraca caerulea lazula, 5.
Gypaetus, 331.
Haeckel, E., cited, 307.
Hall, H. V. M., 127.
Halosoma viridintestinalis, 133.
Hansen, J. H., 173.
Harding, W. A., cited, 205, 217.
Hargitt, C. W., cited, 251.
Haring, Clarence M., 30.
Harless, cited, 143.
Harper, E. H., cited, 227.
Harrison, R. G., 144, 158, 167.
Hawk, Marsh, feathers of, 329–336.
See also Circus hudsonius.
sparrow, 6.
Swainson, 6.
Haemolytic reactions, 48.
Heinicke, F., cited, 144.
Hemiclepsis marginata, 206, 218.
occidentalis, 206, 218; experiments on "parental instinct," 235–240.
tessulata, 206.
Hemiptera, food of meadowlark, 432.
Heron, great blue, 5, 11.
Anthony green, 5, 8, 11, 19, 461.
black-crowned night, 5.
Herpodella otoculata, 217.
Himantopus mexicanus, 5.
Hippocrene, 316, 321.
Hirundo erythrogastra, 5, 6.
His, W., cited, 156.
Histeridae, 427.
Holmes, S. J., 128, 143, 155; acknowledgment of assistance, 191; cited, 173, 178, 200, 204, 227, 251, 265.
Houghton, W., cited, 200, 201.
Hyla regilla, 53, 65, pl. 1, opp. p. 88, 144, 145, 149, pl. 5, opp. p. 152, pl. 6, opp. p. 154, 158, 159, 162, pl. 7, opp. p. 170, pl. 8, opp. p. 172; feeding experiments, with liver and egg yolk, 61; after removal of yolk, 62; effect of, on color and size, 66; effect on growth, of albumen and lecithin, 74; of liver and lecithin, 75; of gliadin, 78; of resorcin, 79.
Hymenoptera, food for meadowlark, 433.
Hyperplasia, 37.
Ichneumonidae, 434.
Icteria virens longicauda, 5.
Icterus bullocki, 5, 6, 18.
Immunity to Epithelioma contagiosum, development of, 40.
Insectivorous birds, 15, 470.
Insects, 442, 443, 446, 470, 471; destroyed by meadowlark, 472; outbreaks of, 2, 14, 16, 19, 492; protective adaptations of, 480.
Jassidae, food for meadowlark, 432.
Jay, blue-fronted, 457.
Jennings, H. S., cited, 200, 250, 251, 265.
Johnson, Myrtle E., 53.
Julus, food for meadowlark, 436.
Killdeer, 5, 6, 8, 11, 18, 19, 461.
Kincaid, T., 128.
Kingbird, western, 5, 6, 7, 8, 19, 457, 461.
Kofoid, C. A., 21, 397; acknowledgment of assistance, 18, 30, 128, 137, 173, 199, 308, 380.
Lactic acid, fatigue substance in leeches, 284.
Laguna Beach, California, 127.
Land-birds, 4.
Land leech of Japan, notes on, 230.
Lanius ludovicianus gambeli, 5, 6, 18.
Lark, California horned, 5, 6, 8, 19, 380, 461.
Lark sparrow, western, 5.
Lathrop, F. H., cited, 267.
Lecithin, effect of, on tyrosinase reaction, 54, 69; on pigmentation, 73, 84.
Lecythorhynchus marginatus, 131.
Lee, F. S., cited, 267, 282, 285.
Leech, blood, its use in medical practice, 191.
Leech, land, of Japan, notes on, 230.
Leech behavior, during the breeding season, 233; influence on, of operation experiments, 245; effect on, of nicotine, 274; of cocaine, 278; chloretone as a depressant, 279; effect on, of magnesium sulphate, 280; of combined stimuli, 285; influ-

ence of food juices on reaction to contact, 285; influence of internal states, 290–295; modifiability in, 295; summary of, 297–300.

Leeches, Behavior of with Especial Reference to its Modifiability, 197.

Leeches, as weather prognosticators, 200; incubating eggs, 201, 203; hypodermal impregnation, 202; as human parasites in Palestine, 205; categories of movements in, 208; random movements, 209; looping response, 210; swimming response, 211; respiratory movements, 212; food of, 217; scavengers in the genus Dina, 218; extreme sensitivity to various stimuli, 221; phototaxis in, 227; rheotaxis in, 227; young leeches, behavior of, 241; thigmotaxis in, 232, 241; diurnal rhythm, 240; function of the brain, 248; acclimatization of leeches, to repeated jars, 261; to successive shadows, 263; causative factors of, 265; physiological bases for reactions of, 250; causes producing fatigue in, 284; effect of combined stimuli: influence of food juices on reaction to contact, 285; effect of light and contact, 288; starved leeches, reactions of, 287, 291; well-fed leeches, reactions of, 288, 290. *See also* Collections of Leeches, *and* Leeches, Reactions of.

Leeches, reactions of, general, 199; righting, 214; to gravity, 230; physiological bases for, 250; influence of food juices on reaction to contact, 285; of starved leeches, 287, 291; of well-fed leeches, 288, 290.

Lemmermann, E., cited, 21.

Lepidoptera, food of meadowlark, 430.

Leptotene stage in spermatogenesis, 516.

Leucophores, pl. 6, opp. p. 154.

Lewis, M. R., and W. H., cited, 157.

Leydig, F., cited, 143.

Limnatis nilotica, 205.

Linnet, 5, 379.

Lister, cited, 143.

Literature on leeches, resumé of, 199.

Little, Etta V., 307.

Lizzia, 311, 317, 321.

Locust, 1.

Locustidae, 429.

Loeb, J., cited, 144.

Long, J. A., 308, 511.

Looping response in leeches, 210.

Lori rajah, 64.

Lorius garrulus, 64.

Macrobdella decora, 203.

Magnesium sulphate, effect of, on leech behavior, 280.

Malformation in meadowlarks, 477, 492.

Marsh hawk, feathers of, 329–376.

Masterman, E. W. G., cited, 205.

Maturation division in *Aneides lugubris*, 518.

Mayer, A. G., cited, 307.

Meadowlark, the Western (*Sturnella Neglecta*) in California, A Determination of the Economic Status of, 377.

Meadowlark, western, 5, 6, 7, 8, 10, 15, 17, 18, 19, 400, 461, 476, 491; abundance of, 402; albinism in, 479, 492; damage caused by, 404, 408; death rate, 479, 492; digestion, 412; economic status, 466; eggs, 404; experiments on captive birds, 409; feces, 437; food habits and requirements, 410, 420–436, 438–439, 449, 451, 452, 453, 455, 457, 460, 487; weed seeds destroyed by, 442, 473; a grasshopper destroyer, 430; habits, 400; incubation and moult, 478; insects destroyed by, 472; legislation regarding, 475, 476; malformation, 477, 492; nesting habits, 404; nestlings, 404, 411, 447; non-game bird, 472; parasitism in, 477, 492; protection of crops from, 474; song, 387; stomach contents, 413, 418, 420; stomach examinations, 491; variation in, 477.

Melanin, 147.

Melanoplus differentialis, 2, 3, 430.

Melicertum, 307.

Meloidae, 427.

Melospiza melodia heermanni, 5, 6.

Membracidae, food for meadowlark, 432.
Mendelian factor hypothesis, 55.
Messor, food for meadowlark, 433.
Michael, E. L., 89.
Michener, J. R., 21.
Millipedes, food of meadowlark, 436.
Milvus, 331.
Mimus polyglottos leucopterus, 6.
Minot, C. S., cited, 385.
Mockingbird, western, 6.
Modifiability in leech behavior, 295.
Modifications and Adaptations to Function in the Feathers of *Circus Hudsonius*, 329.
Moltschanov, L. A., cited, 206.
Mono-potassium phosphate, as a fatigue substance, 283.
Moore, J. P., acknowledgment of assistance, 199; cited, 206.
Moquin-Tandon, A., cited, 200.
Morgan, T. H., cited, 245.
Moths, food of meadowlark, 430, 431.
Müller, H., cited, 143.
Mutillidae, 434, 483, 487.
Myrmeleon, food of meadowlark, 436.
Mysis, 177.
  costata, description of, 177.
  oculata, 177.
Neomysis, 177.
  franciscorum, description of, 178.
  rayii, 178.
  vulgaris, 177.
Nicotine, its effect on leech behavior, 274.
Nighthawks, 12.
Noctuidae, 431.
Numenius hudsonius, 6.
Nycticorax nycticorax naevius, 5.
Nymphalidae, 431.
Observations on Isolated Living Pigment Cells from the Larvae of Amphibians, 143.
Oceania, 321.
Ocellus of *Polyocrhis*, 311; pigment, 312; lens, 312, 316; arrangement of parts, 314; epithelial cells, 314; pigment cells, 315; sensory cells, 315; spindle-shaped sense cells, 316; multipolar cells, 318; nerve ring, 319.
Oil-gland of Circus hudsonius, 362.
Onchocalanus **latus**, 183.
Onchorhynchus keta, 174.
Operation experiments, their influence on leech behavior, 245.
Oppel, A., cited, 156, 157, 166.
Oriole, Bullock, 5, 6, 7, 8, 12, 18, 19, 461.
Ornithology, economic, 1, 377, 381, 388, 389; history of methods of, 389, 394; comparison of methods of, 397; problems of, 488.
Orthoptera, food of meadowlark, 429.
Otiorhynchidae, 427.
Otocoris alpestris actia, 5, 6, 19.
Owl, burrowing, 5, 6, 8, 18, 461.
Oxyechus vociferus, 5, 6, 19.
Pallene **californiensis**, 131; description, 133; measurements, 135.
  empusa, 135.
  laevis, 135.
Parapomala calamus, 4.
Parasitism, problem of, in meadowlark, 477, 492.
Parasynaptic Stages in the Testis of *Aneides Lugubris* **(Hallowell)**, 511.
Parental instinct, experiments on, in leeches *Glossiphonia stagnalis*, and *Hemiclepsis occidentalis*, 235–240.
Parker, G. H., cited, 201, 227.
Passer domesticus, 5, 6, 18.
Passerina amoena, 5.
Pearl, R., cited, 216.
Pelobates, 59.
Pentatomidae, 432, 483.
Peridiniella, 27.
Peridinium, 22.
  achromaticum, 27.
  umbonatum, 27.
Pernis, 331.
Peters, A., cited, 158.
Petrochelidon lunifrons lunifrons, 5, 6, 19.
Phalangidae, food of meadowlark, 435.
Phoebe, black, 5, 8, 19, 461.
  Say, 457.
Phototaxis in leeches *Dina microstoma* and *Glossiphonia stagnalis*, 223.
Phoxichilidiidae, 133.
Phoxichilidium femoratum, 133.
Phyllospadix, 127, 129.
Physiological bases for reactions of leeches, 250.

Pigment Cells from the Larvae of Amphibians, Observations on, 143.
Pigment formation, 54; effect upon, of food, and of lecithin, 54; current theories of, 54.
Pigment Formation in Amphibian Larvae, The Control of, 53.
Pigmentation, relation to, of amount of nutrition, 59, 84; effect on, of various kinds of food, 63; effect on, of lecithin, 73, 84; of organic substances, 76; of changes in light, heat, and food, 82.
Podisus, 483.
Pogonomyrmex, food for meadowlark, 433.
Polar orientation, in spermatocyte of *Aneides lugubris*, 517.
Polyorchis campanulata, 308.
minuta, 308.
penicillata, 307, 308.
pinnatus, 307.
Polyorchis penicillata, methods of study, 308; structure, 309; manubrium, gonads, tentacles, 310; eye-spot or ocellus, 311; peripheral nervous system, 317; bibliography, 321. *See also* Ocellus.
Polyorchis penicillata, The Structure of the Ocelli of, 307.
Pomona College, Marine Laboratory, 127.
Pontobdella muricata, 203, 239.
Porcellis scaber, food of meadowlark, 346.
Powder-down, 331, 333, 362.
Primary, of remiges, 340, 362.
Protective adaptation, of insects, 480, 492.
Protective coloration, 487.
Protozoan cell parasites, 39.
Pterylography, 331.
Pycnogonida, distribution of, 127; bibliography of, 138; of the West Coast of North America, key to, 131.
Pycnogonida from the Coast of California with Descriptions of Two New Species, 127.
Pycnogonum stearnsi, 133.
Quill, of down feathers, 332; of wing coverts, 344.
Ramus, of remiges, 340.
Rana sp., 65, pl. 1, opp. pp. 88, 158, 159, 162, 163, pl. 7, opp. p. 170; feeding experiments, with liver and egg yolk, 61; after removing yolk, 62; effect on growth, of albumen and lecithin, 73; of liver and lecithin, 74; of liver, yolk, and gliadin, 78.
Rana tadpoles, 80.
Random movements in leeches, 209.
Rectrices, 350; shaft, vanes, tail feathers, proximal barbules, distal barbules, barbs, 350; downy structure, 363.
Reduviidae, food for meadowlark 432, 483.
Red-wing, bicolored, 5, 6, 8, 10 15, 17, 18, 380, 461.
tricolored, 6, 19.
Regerhinus, 331.
Remiges, macroscopic structure of, 336; calamus, 336; shaft, 337; barbs, 337; inner vane, 338; outer vane, 339; secondaries, 340.
microscopic structure of, 340; primary, 340, 362; barb, ramus, barbules, 340; proximal barbules, 341, 342; distal barbules, 341, 342, 343; secondaries, 343; downy structure, 363.
Respiratory movements in leeches, 212.
Rheotaxis in leeches, 227.
Rhythm, diurnal, in leeches, 240.
Riddle, O., cited, 56, 57, 58, 63.
Righting reactions in leeches, 214.
Ritter, W. E., 128.
Roadrunner, 380.
Robin, western, 380.
Romanes, G. J., cited, 64, 317, 319.
Roup, relationship to epithelioma contagiosum, 41; development of, in immune fowls, 42.
Roux, 155.
Rusk, G. Y., acknowledgment of assistance, 30.
Rynberk, G. van, 144.
Sagitta californica, **n. sp., from the San Diego Region, Including Remarks on its Variation and Distribution,** 89.
Sagitta californica, description of, 90; distribution of, 122; collarette, 91; anterior fin, 91; posterior fin, 92; vestibular ridge, 92; anterior teeth, 92; posterior teeth, 92; seizing jaws, 92; ovaries, 93; measurements, table of, 94–101;

variation and correlation in proportional measurements, 102; variations in width of body, 103; in length of ventral ganglion, 104; in interval from anterior to posterior fin, 106; in interval from posterior fin to seminal vesicle, 107; in length of ovary, 108; in length of tail, 110; in number of anterior teeth, 113; in number of posterior teeth, 115; in number of seizing jaws, 118.
San Diego Region, the Fourth Taxonomic Report on the Copepoda of the, 181.
Sarsia, 307, 316, 317, 319.
Sayornis nigricans, 5, 19.
sayus, 457.
Scarabaeidae, 427.
Schizopoda, On Some Californian, 173.
Schizopoda, bibliography of, 179.
Scolecithrix **aculeata**, 183.
elephas, 185.
longirostris, 185.
mollis, 186.
obscura, 184.
Scolopendra, food of meadowlark, 436.
Scorpions, 484.
Secondaries, of remiges, 340, 343.
Sensitivity of leeches to various stimuli, 221.
Serum, haemolytic reactions, 48.
Shaft of remiges, 337; of wing coverts, 344, 345, 346; of rectrices, 350; of contour feathers of trunk, 352. *See also* Aftershafts.
Sherrington, C. S., cited, 260.
Shore-birds, 4, 11, 13.
Shrike, California, 5, 6, 7, 8, 11, 18, 19, 461.
Sialia mexicana occidentalis, 6.
Silphidae, 427.
Siriella anomala, 176.
inornata, 175, 176.
media, 175, 176.
pacifica, description of, 175.
Smith, Amelia C., cited, 216.
Smith, H. M., cited, 173.
Snook, Harry J., 511.
Solger, B., cited, 144.
Sow-bugs, food of meadowlark, 436.
Sparrow, English, 5, 6, 8, 11, 18, 461.
song, 5, 6.
western lark, 5, 6, 12.
Speotyto cunicularia hypogaea, 5, 6, 18.
Spermatocyte of *Aneides lugubris*, V-figures, and Y-figures in cells of, 516, 523, 524; horse-shaped loops, 517; polar orientation, 517; first maturation division, 518; synapsis, 521.
Spermatogonia of *Aneides lugubris*, 513, 523, 524.
Spermatogenesis, amphitene stage, 516; leptotene stage, 516.
Sphegidae, 434.
Sphenophorus, 428.
Sphingidae, 431.
Spiders (Arachnida), food of meadowlark, 435.
Spiraulax, 26, 27.
Staphylinidae, 427.
Staurostoma arctica, 311.
Stenopelmatus, 429, 430.
Stilt, black-necked, 5.
Stimulation of *Dina microstoma*, different responses in, to the same contact stimulation, 253-256; determining factors of the different response to the same stimulus, 256; intensity of stimulus, 256; localization of stimulus, 257; position of the body, 257; tonus of the organization, 258; chain reflexes, 259; fatigue from repeated contact stimuli, 267.
Stink-bugs, protective characteristics of, 483.
Stomach contents of birds, 7, 9, 10.
Structure, The, of the Ocelli of Polyorchis Penicillata, 307.
Structure and Relationships of *Dinosphaera Palustris* (Lemm.), On the, 21.
Strychnine, its influence on *Dina microstoma*, 273.
Sturnella neglecta, 5, 6, 18, 377, 400, 457, 476, 490, 491.
Swallow, barn, 5, 6, 12.
cliff, 5, 6, 8, 12, 19, 461.
Sweet, Clifford D., 29.
Swimming response in leeches, 211.
Synapsis of spermatocyte of *Aneides lugubris*, 521.
Syngnathus, 144.
Syncoryne, 321.
Syrphus, food of meadowlark, 434.
Tadpoles, Behavior of Ectodermic Epithelium of, When Cultivated in Plasma, 155.
Tail feathers, 361, 365; of rectrices, 350.

Tail coverts, upper, 354; under, 356.
Tanystylum intermedium, 131, 132.
Taxonomic Report, Fourth, On the Copepoda of the San Diego Region, 181.
Tenebrionidae, 427.
Testis of *Aeneides lubugris* (Hallowell), Parasynaptic Stages in, 511.
Thigmotaxis, in leeches, 232; in young leeches, 241.
Thomomys angularis, 11.
Thysanoessa, 173.
  gregaria, 174.
  raschii, 174.
  spinifera, 174.
Tipula, food of meadowlark, 434.
Tornier, G., cited, 59.
Torrey, H. B., acknowledgment of assistance, 54.
Tubularia, 137.
Turris, 321.
Tyrannus verticalis, 5, 6, 18, 457.
Tyrosinase reaction, effect on, of lecithin, 54, 69; of blood serum, 72; of organic substances, 76.
Uexküll, J. von, cited, 202.
United States Bureau of Biological Survey, 378.
United States Bureau of Fisheries, 173.
United States Department of Agriculture, 379, 392.
Vane, of remiges, inner, 338, outer, 339; of wing coverts, 346; of rectrices, 350; of contour feathers of trunk, 352.
Verril, A. E., cited, 203.
Vespidae, 434.
Virchow, R., cited, 143.
Wagner, G., cited, 265.
Wallace, A. R., cited, 64.
Wasps, food of meadowlark, 433, 483.
Water-birds, 4, 11, 13.
Weed seeds, destroyed by meadowlark, 442, 473.
Weevils, 428.
Western meadowlark. *See* Meadowlark.
Weisman's general selection theory, 54.
Whitman, C. O., cited, 202, 219, 220, 221, 230, 233.
Wild life, conservation of, 383.
Wing coverts of Circus hudsonius, 344; greater upper coverts, 344, 364; quills, calamus, shaft, distal barbules, proximal barbules, 344; greater under coverts, 345, 364; calamus, shaft, barb, barbules, 345; middle and lesser upper coverts, 346; humerals, 347, 365; middle and lesser under coverts, 347, 348.
Wireworms, 428.
Wittich, von, cited, 143.
Xanthocephalus xanthocephalus, 6.
Xanthophores, 149.
Yerkes, Ada W., cited, 251.
Yerkes, R. C., 200.
Zenaidura macroura marginella, 5.
Zimmermann, K. W., 144.

ERRATA

Page 27. *For* Peridinum *read* Peridinium.
Page 30. *For* avain *read* avian.
Page 67. *For* later *read* latter (line 9).
Page 149, first line. *For* where *read* while.
Page 245, line 8 from bottom. *For* Hirshler *read* Hirschler.
Page 361, line 21. *For* diverse *read* divers.
Page 385. Omit comma after *record,* line 12.
Page 386, line 6. *For* period after "outbreaks" *read* comma.
Page 457, line 13. *For* stellari *read* stelleri.

5. On the Skeletal Morphology of *Gonyaulax catenata* (Levander), by Charles Atwood Kofoid. Pp. 287-294, plate 18.
6. Dinoflagellata of the San Diego Region, V. On *Spiraulax*, a New Genus of the Peridinida, by Charles Atwood Kofoid. Pp. 295-300, plate 19.
   Nos. 4, 5, and 6 in one cover. September, 1911 ..... 1.50
7. Notes on Some Cephalopods in the Collection of the University of California, by S. S. Berry. Pp. 301-310, plates 20-21. September, 1911. .10
8. On a Self-Closing Plankton Net for Horizontal Towing, by Charles Atwood Kofoid. Pp. 311-348, plates 22-25.
9. On an Improved Form of Self-closing Water-bucket for Plankton Investigations, by Charles Atwood Kofoid. Pp. 349-352.
   Nos. 8 and 9 in one cover. November, 1911 ..... .40
   Index, pp. 353-357.

Vol. 9.

1. The Horned Lizards of California and Nevada of the Genera *Phrynosoma* and *Anota*, by Harold C. Bryant. Pp. 1-84, plates 1-9. December, 1911 ..... .70
2. On a Lymphoid Structure Lying Over the Myelencephalon of *Lepisosteus*, by Asa C. Chandler. Pp. 85-104, plates 10-12. December, 1911. .25
3. Studies on Early Stages of Development in Rats and Mice, No. 3, by E. L. Mark and J. A. Long. The Living Eggs of Rats and Mice with a Description of Apparatus for Obtaining and Observing Them (*Preliminary paper*), by J. A. Long. Pp. 105-136, plates 13-17. February, 1912 ..... .30
4. The Marine Biological Station of San Diego, Its History, Present Conditions, Achievements, and Aims, by Wm. E. Ritter. Pp. 137-248, plates 18-24, and 2 maps. March, 1912 ..... 1.00
5. Oxygen and Polarity in *Tubularia*, by Harry Beal Torrey. Pp. 249-251. May, 1912 ..... .05
6. The Occurrence and Vertical Distribution of the Copepoda of the San Diego Region, with particular reference to Nineteen Species, by Calvin O. Esterly. Pp. 253-340, 7 text-figures. July, 1912 ..... 1.00
7. Observations on the Suckling Period in the Guinea-Pig, by J. Marion Read. Pp. 341-351. September, 1912 ..... .10
8. Haeckel's *Sethocephalus eucecryphalus* (Radiolaria), a Marine Ciliate, by Charles Atwood Kofoid. Pp. 353-357. September, 1912 ..... .05
   Index, pp. 359-365.

Vol. 10. (Contributions from the Museum of Vertebrate Zoology.)

1. Report on a Collection of Birds and Mammals from Vancouver Island, by Harry S. Swarth. Pp. 1-124, plates 1-4. February, 1912 ..... 1.00
2. A New Cony from the Vicinity of Mount Whitney, by Joseph Grinnell. Pp. 125-129. January, 1912 ..... .05
3. The Mole of Southern California, by J. Grinnell and H. S. Swarth. Pp. 131-136, 2 text-figures.
4. *Myotis orinomus* Elliott, a Bat New to California, by J. Grinnell and H. S. Swarth. Pp. 137-142, 2 text-figures.
   Nos. 3 and 4 in one cover. April, 1912 ..... .12
5. The Bighorn of the Sierra Nevada, by Joseph Grinnell. Pp. 143-153, 4 text-figures. May, 1912 ..... .10
6. A New *Perognathus* from the San Joaquin Valley, California, by Walter P. Taylor. Pp. 155-166, 1 text-figure.
7. The Beaver of West Central California, by Walter P. Taylor. Pp. 167-169.
   Nos. 6 and 7 in one cover. May, 1912 ..... .15
8. The Two Pocket Gophers of the Region Contiguous to the Lower Colorado River, in California and Arizona, by Joseph Grinnell. Pp. 171-178. June, 1912 ..... .15
9. The Species of the Mammalian Genus *Sorex* of West-Central California, with a note on the Vertebrate Palustrine Faunas of the Region, by Joseph Grinnell. Pp. 179-195, figs. 1-6. March, 1913 ..... .15
10. An Account of the Birds and Mammals of the San Jacinto Area of Southern California, with Remarks Upon the Behavior of Geographic Races on the Margins of Their Habitats, by J. Grinnell and H. S. Swarth. Pp. 197-406, pls. 6-10. October, 1913 ..... 2.00
    Index, pp. 407-417.

Vol. 11. 1. Birds in Relation to a Grasshopper Outbreak in California, by Harold C. Bryant. Pp. 1-20. November, 1912 .20
2. On the Structure and Relationships of *Dinosphaera palustris* (Lemm.), by Charles Atwood Kofoid and Josephine Bigden Michener. Pp. 21-28. December, 1912 .10
3. A Study of Epithelioma Contagiosum of the Common Fowl, by Clifford D. Sweet. Pp. 29-51. January, 1913 .25
4. The Control of Pigment Formation in Amphibian Larvae, by Myrtle E. Johnson. Pp. 53-88, plate 1. March, 1913 .35
5. *Sagitta californica*, n. sp., from the San Diego Region, including Remarks on Its Variation and Distribution, by Ellis L. Michael. Pp. 89-126, plate 2. June, 1913 .35
6. Pycnogonida from the Coast of California, with Description of Two New Species, by H. V. M. Hall. Pp. 127-142, plates 3-4. August, 1913. .20
7. Observations on Isolated Living Pigment Cells from the Larvae of Amphibians, by S. J. Holmes. Pp. 143-154, plates 5-6.
8. Behavior of Ectodermic Epithelium of Tadpoles when Cultivated in Plasma, by S. J. Holmes. Pp. 155-172, plates 7-8.
Nos. 7 and 8 in one cover. September, 1913 .30
9. On Some Californian Schizopoda, by H. J. Hansen. Pp. 173-180, pl. 9. November, 1913 .10
10. Fourth Taxonomic Report on the Copepoda of the San Diego Region, by Calvin O. Esterly. Pp. 181-196, pls. 10-12. November, 1913 .15
11. The Behavior of Leeches with Especial Reference to Its Modifiability, A. The General Reactions of the Leeches *Dina microstoma* Moore and *Glossiphonia stagnalis* Linnaeus; B. Modifiability in the Behavior of the Leech *Dina microstoma* Moore, by Wilson Gee. Pp. 197-305, 13 text figures. December, 1913 1.00
12. The Structure of the Ocelli of *Polyorchis penicillata*, by Etta Viola Little. Pp. 307-328, plates 13-15. February, 1914 .20
13. Modifications and Adaptations to Functions in the Feathers of *Circus hudsonius*, by Asa C. Chandler. Pp. 329-376, plates 16-20. March, 1914 .50
14. A Determination of the Economic Status of the Western Meadowlark (*Sturnella neglecta*) in California, by Harold Child Bryant. Pp. 377-510, plates 21-24, 5 text figures. February, 1914 1.25
15. Parasynaptic Stages in the Testis of *Aneides lugubris* (Hallowell), by Harry James Snook and J. A. Long. Pp. 511-528, plates 25-26, 1 text fig. April, 1914 .25

Vol. 12. 1. A Study of a Collection of Geese of the *Branta canadensis* Group from the San Joaquin Valley, California, by Harry S. Swarth. Pp. 1-24, plates 1-2, 8 text figs. November, 1913 .30
2. Nocturnal Wanderings of the California Pocket Gopher, by Harold C. Bryant. Pp. 25-29, 1 text fig. November, 1913 .05
3. The Reptiles of the San Jacinto Area of Southern California, by Sarah Rogers Atsatt. Pp. 31-50. November, 1913 .20
4. An Account of the Mammals and Birds of the Lower Colorado Valley, with Especial Reference to the Distributional Problems Presented, by Joseph Grinnell. Pp. 51-294, plates 3-13, 9 text figs. March, 1914. 2.40

Vol. 13. 1. The Schizopoda of the San Diego Region, by Calvin O. Esterly. Pp. 1-20, plates 1-2. April, 1914 .15
2. A Study of the Occurrence and Manner of Distribution of the Ctenophora of the San Diego Region, by Calvin O. Esterly. Pp. 21-38. April, 1914 .15
3. A New Self-Regulating Paraffin Bath, by C. W. Woodworth. Pp. 39-42, 2 text-figures. April, 1914 .05

SMITHSONIAN INSTITUTION LIBRARIES
3 9088 01257 4158